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GALATHEA REPORT

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Volume 4

Scientific Results
of The Danish Deep-Sea Expedition
Round the World 1950-52

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POGONOPHORA III

The Genus Lamellisabella

By J. B. KIRKEGAARD
Zoological Museum, Copenhagen

Introduction

In 1957 a paper by Ivanov appeared with descriptions of several new species of Pogonophora from the north-western part of the Pacific Ocean. In this report the genus *Lamellisabella* comprises two species, *L. zachsi* and *L. johanssoni*; and according to Ivanov the differences between them are very small. In my paper from 1956 I described a find of *L. zachsi* from the Gulf of Panama. This record was so far from the earlier known distribution of this species that it indicated a more worldwide distribution of the Pogonophora species than was hitherto expected. When Ivanov's paper appeared, and I saw how small the differences between the species were, I sent my specimen from the Gulf of Panama to Ivanov and asked him to make a comparison with his material of *L. zachsi* and *L. johanssoni*. Ivanov was kind

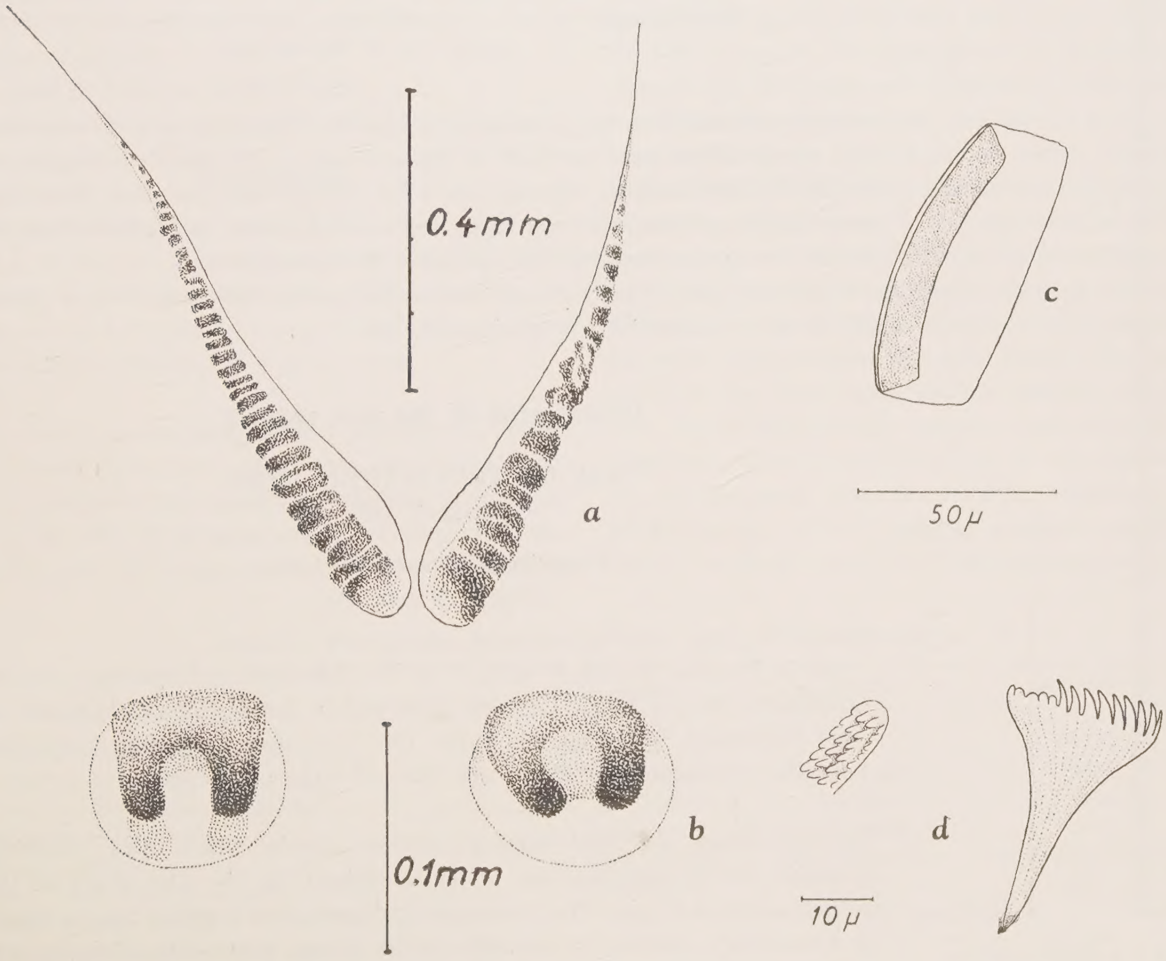

Fig. 1. *Lamellisabella ivanovi* sp. nov. a. Bridle. b. Horseshoeshaped platelets. c. Platelet from the posterior part of the trunk. d. Dendated platelets from the belt. (P. Winther del.).

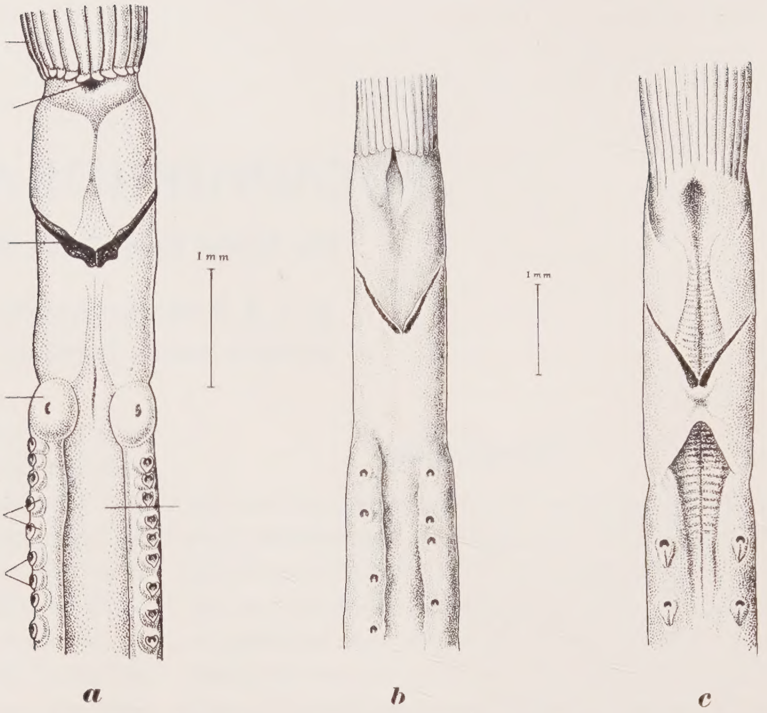

Fig. 3. a. *Lamellisabella johanssoni* Ivanov. (After A. V. IVANOV 1957). b. *Lamellisabella ivanovi* sp. nov. c. *Lamellisabella zachsi* Uschakov. Anterior parts, ventral view. (P. WINTHER del.).

enough to undertake a very detailed investigation of the problem and concluded that the specimen from the Gulf of Panama was a new species belonging to the genus *Lamellisabella*. He sent me a list with several characters from the three species of *Lamellisabella* compared to each other and allowed me to publish it together with the description of the new species.

I am very grateful to Professor IVANOV for his kind help, and it is a pleasure to me to name the new species after him.

Description of the new species

FAM. LAMELLISABELLIDAE

Uschakov, 1933

Lamellisabella ivanovi sp. nov.

(Figs. 1, 2 and 3b).

Material:

Gulf of Panama. St. 724. 5°44′N, 79°20′W. 2950-3190 m. 1 specimen almost complete: 90 × 1 mm (Holotype preserved in the Zoological Museum of the University, Copenhagen). Tube: 150 × $1^{1}/_{2}$ mm. 1 specimen, only the anterior part is present, 35 × 1 mm. Several fragments of tubes.

The 22 tentacles are fused forming a hollow cylinder which opens ventrally through a pit between the base of the tentacles (Fig. 3b). The length of the tentacle-crown is 12 mm. The protosoma and mesosoma together have a length of 3 mm and a width of 1 mm. The bridle is very dark with a brighter anterior edge and bright bands between dark ones at the posterior part (Fig. 1a). This structure is very characteristic of the present species. The two wings of

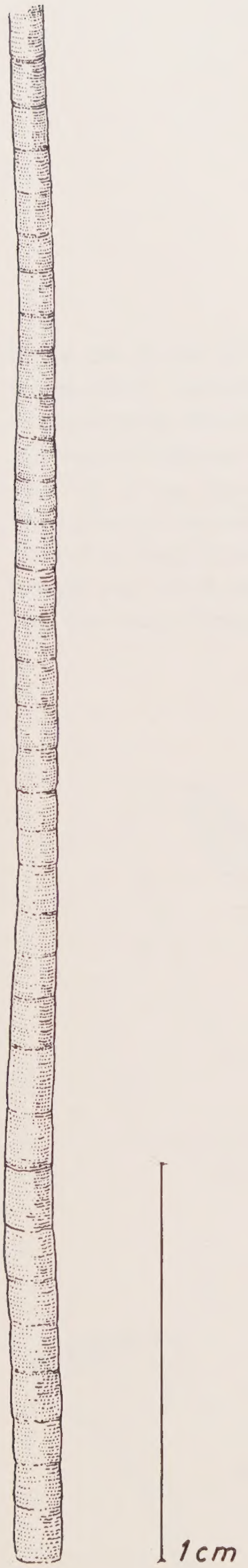

Fig. 2. *Lamellisabella ivanovi* sp. nov. Tube. (P. WINTHER del.).

the bridle do not meet dorsally and are not fused ventrally. The broadest part of the wings is 110 μ. On the border of the anterior part of the ventral groove of the trunk are placed 15-18 horseshoe-shaped chitinized platelets with a diameter of 75 μ (Fig. 1b). In the posterior part of this section are platelets of another type (Fig. 1c) between the horseshoe-shaped ones, and these platelets are the only ones present in the posterior part of the trunk. At the middle of the trunk are two belts, parallel to each other and interrupted on the ventral surface. They consist of rows of small chitinoid platelets with four rows of denticles (Fig. 1d). The preannular section of the trunk is 70 mm long and has a diameter of 1 mm. The length of the postannular section cannot be indicated since the posterior part is absent.

The tube is strongly chitinized, without collars, but faintly segmented (Fig. 2). The colour is brown, light brown and translucent in the upper part and darker in the lower part. It is 150 mm long with a maximum diameter of $1^{1}/_{2}$ mm.

Distribution:

Gulf of Panama, 2950-3500 m.

Discussion

Since the differences between the three known species of the genus *Lamellisabella* are small I find it useful to publish Ivanov's list, which he sent me, to show why he preferred to regard the specimen from the Gulf of Panama as a new species.

As seen from the table below it looks as if *L. ivanovi* is closest related to *L. johanssoni,* since most of the characters are very much alike in these two species, e.g. number of tentacles, length of tentacle-crown, width of bridle-wings, number and size of horseshoe-shaped platelets. In the flat shape of the bridle *L. ivanovi* has more in common with *L. zachsi,* in which the bridle wings also are not fused ventrally as in *L. ivanovi. L. ivanovi* is distinguished from both the other species by the strange structure of the bridle which in both of the known specimens consists of dark bands alternating with bright ones (Fig. 1a).

Since the number of tentacles seems to be a very useful character to distinguish the species of Pogonophora, I agree with Ivanov in separating the three forms discussed above in three species, *L. zachsi* from the Sea of Okhotsk and the Bering Sea, *L. johanssoni* from the Japan Trench and *L. ivanovi* from the Gulf of Panama.

Zoogeographical Remarks

Since my first papers on the Pogonophora were published in 1956, several new records of Pogonophora have turned up. The most comprehensive paper is that of Ivanov (1957), in which he describes 12 new species from the north-western part of the Pacific. In 1956 appeared the description of *Siboglinum ekmani* from the Skagerrak (Jägersten 1956), and in 1958 the description of two new species from the Continental slope south-west of Great Britain (Southward 1958b). These two species, *Siboglinum atlanticum* and *S. inermis* were found together with *S. ekmani* at a depth of 600-1500 m. In the Skagerrak *S. ekmani* is recorded from depths between 500 and 700 m (Kirkegaard 1958a). Until now 26 species are described, most of them from the Pacific area, but also from the Polar Basin and the Atlantic. Moreover, Ivanov has told me that the numerous Soviet expeditions have recorded at least 25 new species, not yet described, from several other localities in the Pacific (e.g. off the Canadian coast), the Indian Ocean, the Polar Basin and in shore waters off the

Table 1. Taxonomic characters of three species of *Lamellisabella.*

	L. zachsi	*L. johanssoni*	*L. ivanovi*
Number of tentacles	29-31	18	20-22
Length of tentackle-crown	27 mm (max)	12 mm (max)	12 mm
Length of Protosoma + mesoma	2.5-3 mm	2-3 mm	3 mm
Diameter of mesosoma	1.3 mm (max)	1 mm (max)	1 mm
Wings of bridle	not fused ventrally	fused ventrally	not fused ventrally
Max. width of bridle wings	60-70 μ	125 μ	110 μ
Shape of bridle wrings	flat	with high ant. edge	flat
Number of horseshoeshaped platelets on each side	22-30	15-25	15-18
Diameter of horseshoeshaped platelets	60 μ	70 μ	75 μ
Tube	not segmented	segmented	segmented

Antarctic.[1] It seems as if the Pogonophora are distributed in all three oceans, and as I wrote in my paper from 1956 I am now more convinced than ever that the Pogonophora occur in every place of the world where the conditions suit this strange group of animals.

---

[1] Since I wrote this, two new papers have appeared, so the total number of described species is now 44.

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DESCRIPTION OF A REMARKABLE DEEP-SEA HERMIT CRAB,

WITH NOTES ON THE EVOLUTION OF THE PAGURIDEA

By TORBEN WOLFF
Zoological Museum, Copenhagen

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INTRODUCTION

During the Danish *Galathea* Deep-Sea Expedition a haul with a large herring otter trawl was carried through in the East Pacific off Costa Rica, at a depth of 3570 m. This trawling was extremely rich, quantitatively as well as qualitatively (WOLFF 1960), including about 126 species of benthic animals, among which were the large deep-sea angler fish *Galatheathauma axeli*, and the ancient mollusc *Neopilina galatheae* (LEMCHE and WINGSTRAND 1959, p. 63).

Among the 10 species of benthic decapod crustaceans were 18 specimens of a remarkable pagurid which for obvious reasons I regarded as a new genus and species. I consequently selected the largest female as holotype, and the description and illustrations were primarily based on this specimen.

During my work with this interesting crustacean I happened to mention it in a letter to Dr. FENNER A. CHACE, Washington. Fortunately, he drew my attention to the short and very imperfect description given by Miss BOONE (1926 a, b) of an animal which she regarded as a primitive macruran crustacean and referred to a new genus and species, *Probeebei mirabilis*, the only representative of the new family Probeebeidae. It was collected by the American *Arcturus* Expedition in 1925. Except for a reference to it in the Zoological Record for 1926 this species has been completely neglected ever since. It was not recognized as a pagurid, and consequently not mentioned by e.g. MELIN in his excellent work on the systematics of the group (1939), in BRONN's Klassen und Ordnungen des Tierreichs (BALSS 1955, 1957 a, 1957 b) or in GORDAN's extensive bibliography of the Paguridea (1956).

On my request Dr. CHACE later furnished me with a photostat copy of BOONE's two papers, which were not obtainable in this country. BOONE's illustration and short description (1926 b) suggested a close relationship between specimens collected by the *Arcturus* and the *Galathea*. Through the courtesy of Dr. JOCELYN CRANE of the New York Zoological Society I was able to borrow the holotype and only specimen of *Probeebei mirabilis*. A comparison between this juvenile specimen and juveniles of the same stage in the *Galathea* material leaves no doubt that they all belong to one species.

Since the holotype is a juvenile and furthermore is somewhat fragmentary I base the detailed description on the previously selected female and thereupon consider the type specimen.

Probeebei Boone, 1926

Probeebei n. gen., Boone 1926 b, p. 73.

Diagnosis:

Carapace completely calcified and considerably swollen. Abdomen distinctly segmented and completely calcified dorsally; segments 2-5 asymmetrical in the female, almost quite symmetrical in the male; tail-fan symmetrical in both sexes; segment 2 much larger than the others. Small flagellum on endopodite of maxillula. No flagellum on exopodite of first maxilliped. Chelipeds weak, the right one a little larger than the left. Peraeopods II and III very elongated. Pleopods 2-5 present on the left side of the adult female, both pleopods 1 present in the adult male; no other pleopods found. 11 pairs of phyllobranchiae.

Type species: *P. mirabilis* Boone.

Probeebei mirabilis Boone, 1926

Probeebei mirabilis n. sp., Boone 1926 a, p. 72; 1926 b, p. 73, fig.

Planopagurus galatheae Wolff, 1960, p. 169, fig. p. 177.

Material:

Galathea St. 716, East Pacific off Costa Rica (9°23′N, 89°32′W), 3570 m, 6 May 1952. Gear: herring otter trawl. Bottom: dark, muddish clay. Bottom temp.: 2,0°C. – Four adult females, three adult males, nine juveniles, and fragments of two specimens; in total eighteen specimens.

Description of adult female.

The carapace (Figs. 1 and 2a) is strongly calcified both on the anterior and posterior portion. The length along the median line (excl. of the rostrum) is exactly the same as the maximum width (excl. of the lateral spines).

The anterior portion (the gastric and cardiac regions) is almost circular in general outline. In front it is separated from the vertical, triangular plate between the rostrum and the eye-stalks (see later) by a low, but sharp crest running from the lateral base of the rostrum to the lateral insertion of the antennae and furnished with a single spine beyond the middle of this stretch. Postero-laterally the anterior portion is separated from the posterior one by two almost parallel grooves on each side (Fig. 2d, 1 and 2) which meet dorsally (3), here forming a deeply cut notch (Figs. 1 and 2a). The notch and one of the two parallel grooves represent the cervical groove (*b* and *c* of Boas 1880, p. 113). A comparison with Boas' figs. 16 and 17 (1926 a) of the carapaces of *Paguristes* and *Mixtopagurus* might indicate that the most median of the two parallel grooves (1) should be the cervical one. However, the broadening of the carapace and its macruran- or even crab-like appearance result in a more lateral passing of the *linea anomurica.* In *Probeebei* (Fig. 2a) as well as in the still more carcinized *Porcellanopagurus* (Borradaile 1916, fig. 2) and the Lithodidae this line runs longitudinally just below the dorsal, spiny part of the carapace, separating this from the lateral parts which will be described below.

The *linea transversalis* of Boas (1926 a, fig. 16) is visible as a faint, uncalcified suture (Fig. 2d, l. t.) which runs immediately behind the median part of the cervical groove. Somewhat before the lateral margin it diverges into two branches, one running obliquely forwards immediately behind groove 2 (Fig. 2d) and ending in the *linea anomurica,* and another which curves backwards closely before the lateral margins (when viewed from above) and also ends in the *linea anomurica.*

Returning to the two parallel grooves 1 and 2 and the question which of them is the cervical one, it would seem that the proximity with which the anterior branch of *linea transv.* follows groove 2 might indicate that 2 is a groove in connexion with *l. transv.* and that, accordingly, 1 must be the cervical groove. But a wide separation between the two parallel grooves of the cervical system and the anterior branch of *l. transv.* is clearly visible in *Lomis hirta* (Bouvier 1895, pl. 13, 7) which resembles a porcellanid crab and is the only species of the family Lomisidae; this family is derived from the symmetrical Pylochelidae, the most primitive pagurids. In *Hapalogaster* which is the most pagurid-like member of the Lithodidae (Bouvier 1895, p. 166) *l. transv.* is much closer to the cervical groove (l. c., pl. 12, figs. 27 and 29) and the conditions seem to correspond closely with those in *Porcellanopagurus.* For *P. edwardsi* Forest (1951, p. 87) suggests that the separation between the calcified and the soft part of the carapace must be "ce qui nous semble correspondre à *linea transversalis* de Boas". This is certainly correct and it must then be the anterior of the branches. The posterior, backwards curved branch found in *Probeebei, Lomis,* and *Hapalogaster* is not mentioned in any description of the species of *Porcellanopagurus.*

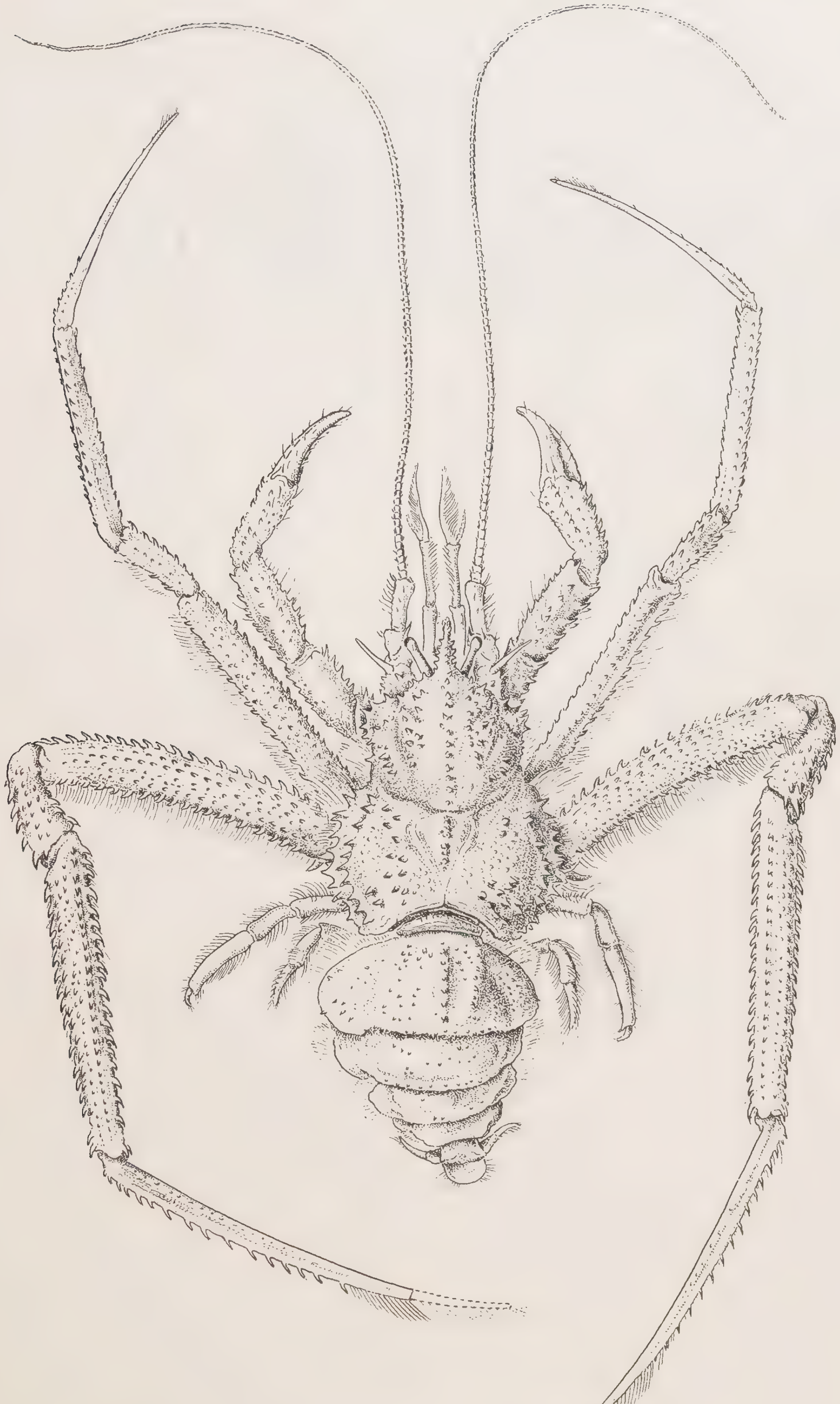
5 cm
Poul H. Winther. 1960.

Fig. 1. *Probeebei mirabilis* Boone; described adult ♀, *Galathea* St. 716.

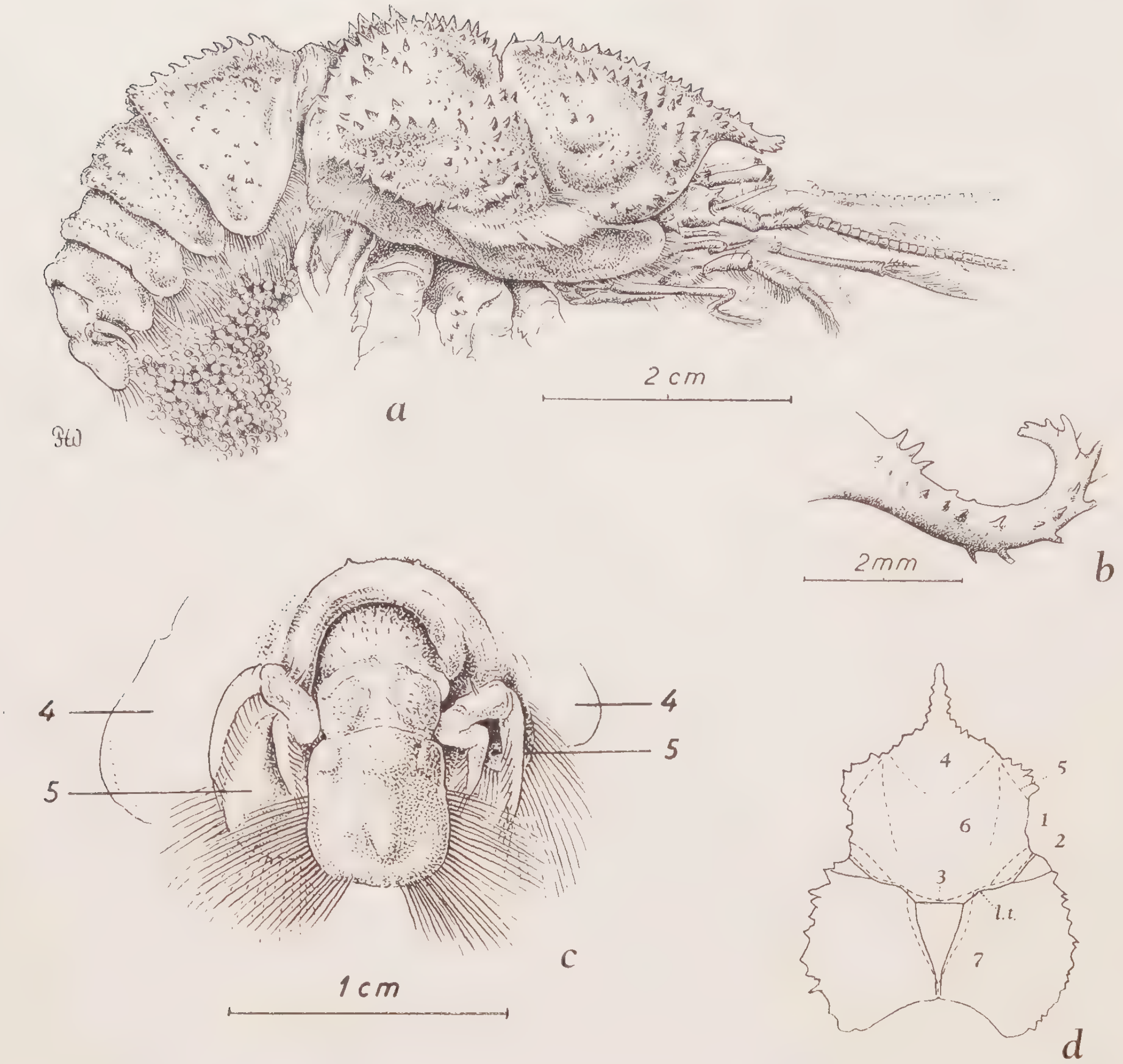

Fig. 2. *Probeebei mirabilis;* a, descr. ♀ from the right side; b, rostrum of juvenile of stage x; c, part of abdominal segment 4, segments 5 and 6, and telson of descr. ♀; d, lines and grooves on the carapace (cf. the text).

By homologizing with these three genera I found it most probable that groove 2 represents the continuation of the cervical groove, and that 1 is a secondarily formed groove, both in *Probeebei* and in *Lomis*. It should be added that in *Pagurus splendescens* (Owen) a system of grooves and lines is found, which, according to the fine illustration in Balss 1913 (pl. II, 2) is almost exactly like that in *Probeebei*. This species will be further discussed below (p. 26).

Besides these grooves, etc. the anterior portion of the carapace is subdivided by the following grooves: Two faint, oblique ones (Fig. 2d, 4) which almost meet in the median line somewhat in front of the middle and together form a broad V with the opening forwards, two grooves running at right angles to these and parallel to and not far from the antero-lateral margins (Fig. 2d, 5), and, finally, two obliquely longitudinal grooves which divide the swollen postero-lateral parts of the anterior portion (6).

There are five, more or less distinct, longitudinal rows of short, stout spines which converge posteriorly, and a short, transverse row in a considerably vaulted area close to the antero-lateral margin.

The rostrum is distinctly set off, and its length is about one-fifth of the carapace (excl. of the rostrum), measured along the median line. Dorsally and laterally it is closely covered with spines, and distally it is curved somewhat upwards (Fig. 2a). It is separated from the eye-stalks by a vertical plate which is as high as half the length of the rostrum.

The plate is broadly triangular with a straight lower margin (because eyes, antennulae and antennae are on the same level); it is devoid of spines.

The posterior portion of the carapace (the hepatic and branchial regions) is considerably broader than the anterior and less vaulted medianly. Here two faint grooves are found (Fig. 2d, 7) which are obviously the cardiobranchial grooves of BOAS (1926a) and which meet at the posterior margin, forming together a narrow V. A little more medianly are two fine sutures which anteriorly originate from *linea transversalis* and converge posteriorly. They probably correspond to those shown in BOAS' fig. 16 (1926 a) of *Paguristes* and are very conspicuous in *Pagurus splendescens* (BALLS 1913, pl. II, 2).

On the posterior portion are seven longitudinal rows of spines, but the row on each side of the median one is rather indistinct. There are also some scattered spines near the posterior margin.

The entire dorsal surface of the carapace is also covered, besides with spines, with many nodules and scattered hairs which are rather long on the anterolateral corners of both the anterior and the posterior portion.

The lateral parts of the carapace are considerably less calcified and almost equally broad throughout (Fig. 2a). They are divided a little before the middle by the line *la*' of BOAS (1880, figs. 141-144) and Figs. 2a and 9 in this paper. Anteriorly they are broadly rounded and bear a row of long setae. Their surface is furnished with rather long, scattered setae, many small nodules and posteriorly a longitudinal row of small spines.

The abdomen (Figs. 1 and 2a) has all seven segments well separated. The terga are strongly calcified, except the sixth and the telson which are rather soft. The five first segments have a thick rounded crest also along the dorsal part of the posterior margin, adding to the armour-like appearance of them. All segments have short scattered hairs.

The first segment is much narrower than the following, and when the abdomen is bent upwards as in Fig. 1, only the posterior, thickened part is visible. If held in its supposed natural position (Fig. 2a), it is a little more than twice as broad as long, with the entire dorsal surface calcified.

Segments 2-5 are asymmetrical, with the left parts somewhat larger than the right so that the abdomen curves to the right side. Laterally the terga are rounded, bent slightly upwards, and with a row of setae. Segment 2 is by far the largest, being as long as segments 3 and 4 and half of 5, measured along the median line. It has one median row of spines which are distinct and two more indistinct pairs of rows. The posterior crest has many rather small spines. Segments 3-5 gradually become narrower, shorter and with fewer spines, the latter having only two or three very small ones.

Segment 6 (Fig. 2c) is symmetrical, about as long as broad, and with a transverse, convex suture in front of the insertion of the uropods. The telson is almost rectangular, a little longer than broad, much convex transversely, and somewhat concave longitudinally. There are three low convexities dorsally.

On the ventral side of the abdomen sternal plates are present on segment 1 in much the same way as in the Pylochelidae (cf. fig. 19 of *Mixtopagurus longicaudalis*, BOAS 1926 a), forming a narrow ring, raised as a rounded heel. On segments 2-5 the sterna are shaped as subtriangular plates, almost as in *Lithodes* (BOAS 1924, fig. 27). The pleopods on the left side are inserted close to the interior margin of the plates and on the right side scarlike impressions of the disappeared pleopods are present – as in the male (Fig. 6b) which has such scars on both sides (cf. p. 19). The vast majority of the ventral side is soft-skinned, with the segments indicated by low, but distinct furrows. The ventral side of the telson is excavated, with a central convexity in front of the anus.

The ocular peduncles are immovably fused with the ophthalmic scales which are very short. The peduncle reaches a little beyond joint 3 of the antennae. It is considerably swollen at the base, the width being here almost twice that of the middle part. It is also somewhat swollen distally. A spine is found on the interior, dorsal part of the scale and on the swollen part of the peduncle, and a third spine dorsally on the peduncle, a little beyond the middle. It has also several long setae dorsally on the distal half. The corneal surface is moderately large, preferably situated on the outer, ventral side of the apex, dark brown, and apparently with well developed ocelli.

The antennulae (Fig. 3a) of the typical shape. Joint 2 is one-fifth longer than joint 1, joint 3 about twice as long as joint 1. This has a small distal spine on the exterior side and a larger one beyond the middle. Distally on the dorsal side is a double spine. Besides it has many long, feathered setae. The upper (outer) flagellum consists of about 25 joints, the lover (inner) of 6 subequal joints.

The antennae are also typically shaped. Joint 1 hardly visible from above, but ventrally almost as long as broad. On the outer and ventral side is a row

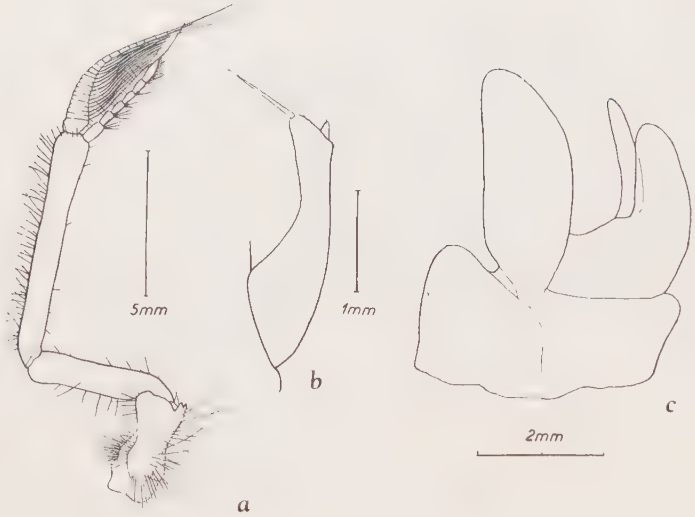

Fig. 3. *Probeebei mirabilis;* a, left antennula of descr. ♀ from inside; b-c, endopodite of maxillula and first maxilliped of dissected ♀ (all setae have been omitted in the maxilliped).

of three spines, and the antennal gland opens on a rounded process on the inner corner. Joint 2 is somewhat broader than long, with one small and three larger spines on the outer margin and a dorsal spine distally. Joint 3 with a strong spine on the inner corner, joint 4 short and unarmed, but with many setae as joint 5. This is almost as long as joints 2-4 combined; it is somewhat widened towards the distal end. The antenna scale is slender, rod-like and furnished with long setae; it is almost as long as joint 5. The flagellum almost twice as long as the entire body and with short and stout, spine-like setae on the numerous joints (about 140).

The mouthparts. I have compared the mouth appendages with those of *Pagurus bernhardus*[1] and *Parapagurus pilosimanus* and found them fairly equal.

The mandible differs from that of *bernhardus* in having more pronounced teeth on the oral end and joint 3 of the palp relatively smaller. From *pilosima-*

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[1] The recent, approved nomenclature has been followed (cf. FOREST 1958).

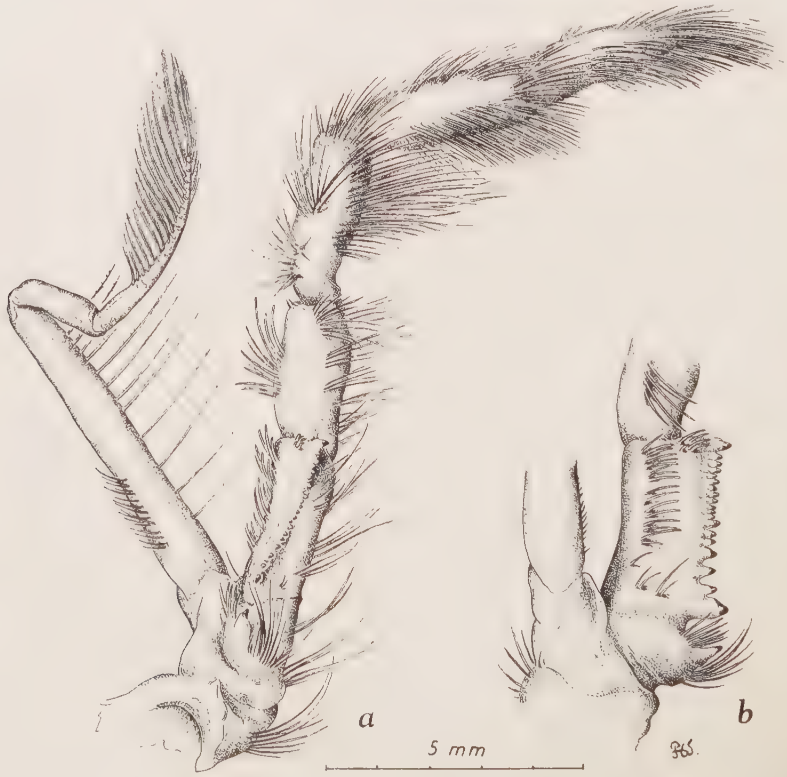

Fig. 4. *Probeebei mirabilis,* dissected ♀; a, left third maxilliped from inside; b, *crista dentata* from in front.

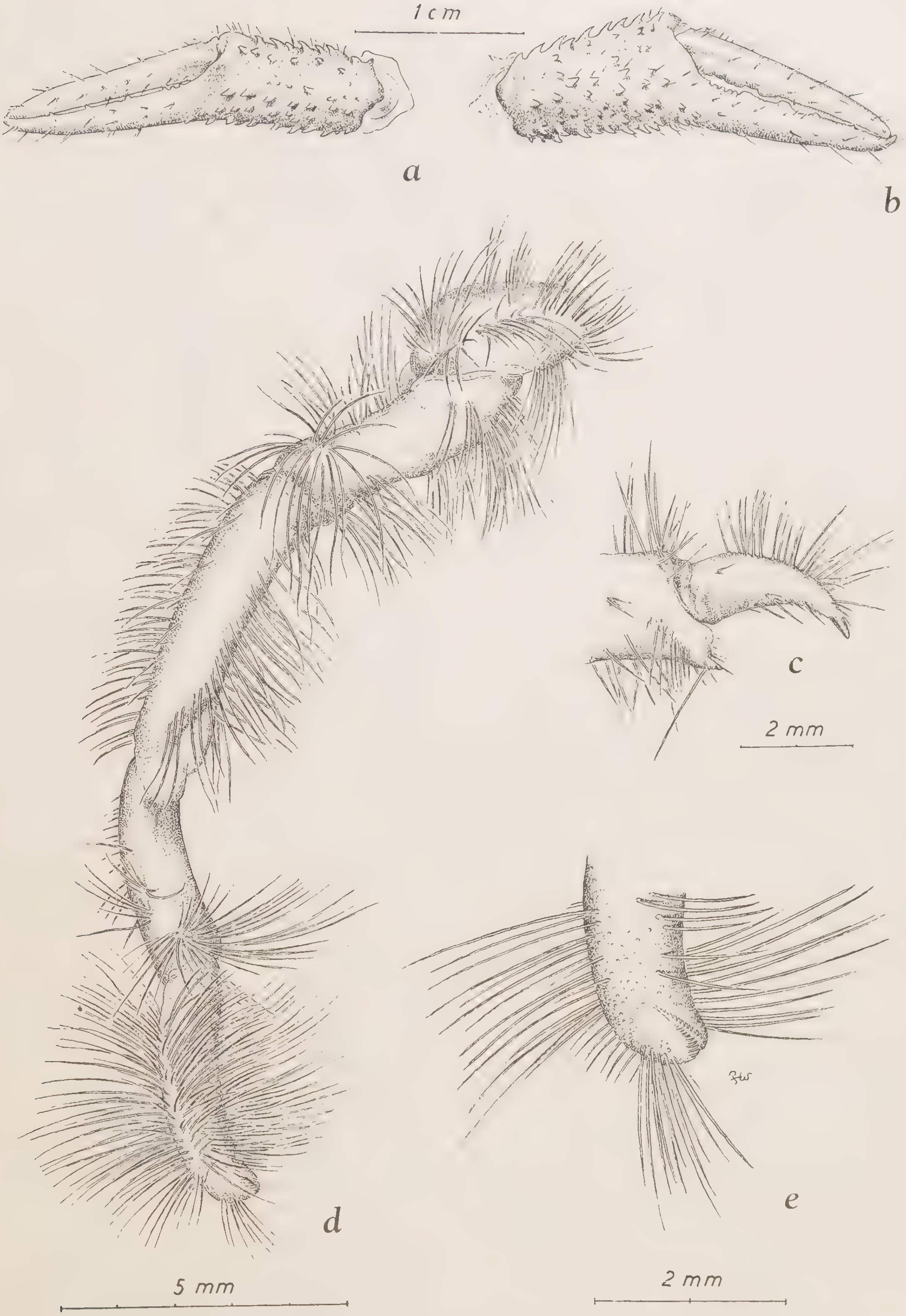

Fig. 5. *Probeebei mirabilis;* a-b, left and right cheliped of descr. ♀; c, distal end of left peraeopod IV of descr. ♂, seen from in front; d, left peraeopod V of descr. ♂, from behind; e, distal end (some setae left out).

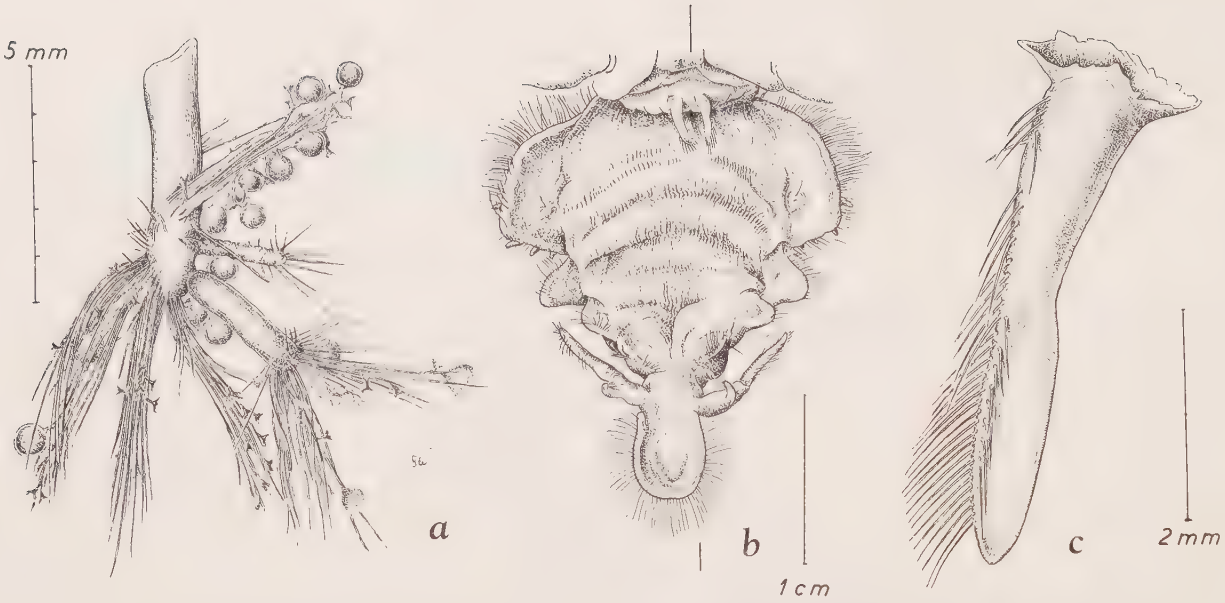

Fig. 6. *Probeebei mirabilis;* a, left pleopod 4 of dissected female from behind (most of the eggs have been removed); b, abdomen of ♂ from below (the short lines above and below the drawing denote the longitudinal axis of the entire animal); c, left pleopod 1 of the same ♂ from inside.

nus it only differs in having a beautiful rosy tinge on the oral part.

The maxillula differs from that of *bernhardus* in having the coxa somewhat more rectangular, the endopodite comparatively narrower (fig. 3b), and the flagellum (appendix) on the latter still smaller, i.e. almost as in *Pylopagurus* (Boas 1924, fig. 18a). *P. pilosimanus* has no trace of a flagellum.

The maxilla in *mirabilis* and *pilosimanus* differs from that of *bernhardus* in having the endopodite reaching beyond the distal endite and the exopodite considerably narrower, tapering towards the proximal and distal ends, and with a constriction almost midway on the outer margin.

The first maxilliped of *bernhardus* (and *Pylopagurus)* has on the exopodite a well developed flagellum which is completely absent in *pilosimanus* and *mirabilis* (Fig. 3c). The exopodite ends a little more abruptly in the latter.

The second maxillipeds are almost equal, but in *bernhardus* the peduncle of the exopodite is less than twice as long as the longest joint (merus) of the endopodite, while in *pilosimanus* and *mirabilis* it is nearly three times as long.

The third maxilliped of *mirabilis* (Fig. 4) differs in being considerably more slender, the teeth of the *crista dentata* are more numerous (about 20) and of less uniform size (Fig. 4b), and merus is on the whole more compressed. Furthermore, the teeth on the distal half of the inner, dorsal side of merus and the distal spine on carpus, found in *bernhardus,* are not present. The peduncle of the exopodite does not reach the distal end of carpus in *bernhardus;* it reaches as far as carpus in *pilosimanus,* and somewhat beyond carpus in *mirabilis.*

The chelipeds are unusually weak. Like the carapace they are armed with scattered setae and spines, some of which are placed in rows. On the ventral margin of both ischium and merus are three or four especially long and pointed spines. Both chelae (Fig. 5a-b) are narrow and pointed, dactylus being more than half as long as propodus. The right cheliped is only slightly longer and heavier than the left.

Peraeopods II and III are almost uniform in shape (dactylus of prp. III is relatively a trifle longer than that of II). The total length of prp. III is almost one and a half times that of II. The coxae are cylindrical and very large; they meet almost in the median line. Ventrally they have a row of rather few spines along the proximal and distal margins. One of the spines in the latter row is exceptionally long, and this is also the case with the distal, posterior spine on ischium. Besides the usual scattered setae there is, especially on merus, a dense row of setae, considerably longer on the hind than on the front margin. Only coxa of the *left* prp. III has a sexual opening.

Peraeopod IV is about as long as the greatest width of the carapace. There are two inner, distal spines on coxa and three inner ones on merus. At the end of propodus is a strong spine below dactylus which, however, works in another plane (behind the

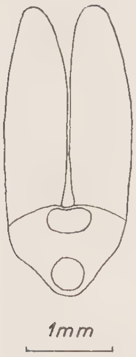

Fig. 7. *Probeebei mirabilis;* section of gill.

spine) so that there is no chela (Fig. 5c). The majority of the many setae on the leg is located along the margins.

Peraeopod V is as shown in Fig. 5d. There are no spines, but a great many setae. Distally is a very tiny, mouth-shaped chela with the "jaws" finely serrated (Fig. 5e).

The pleopods (Fig. 6a) are of equal size. The endopodite is one-sixth longer and twice as broad as the exopodite.

The uropods (Fig. 2c) are practically symmetrical, the right (strangely enough) being perhaps a little bigger than the left. Both the exopodite and the endopodite are sickle-shaped, the former is twice as long and broad as the latter and has along the entire outer margin a narrow band of tiny spines, a rudiment of the file-like surface of other pagurids. The surface of the endopodite is perfectly smooth, except for a row of setae along the inner margin.

Gills. There are 11 gills on each side. The branchial formula is exactly as in *Pagurus* Fabr. (= *Eupagurus* Brandt) and *Lithodes* (Calman 1909, p. 280), i.e. with two arthro-branchiae on maxilliped 3 and each of peraeopods I-IV; prp. IV besides with one pleurobranchia. They are of the phyllobrancheate type, with the branches of each pair regularly oval and equally large (Fig. 7).

Ova. Considering the abyssal environment of this species the number of eggs is remarkably large and their size unusually small, the average diameter being 1.0 mm.

Colour. Notes and colour photographs made on freshly caught specimens give the colour of the legs as a bright orange, and that of the carapace and abdomen of a somewhat lighter orange. The juveniles were still lighter. The eggs had a dark red colour.

Size. The described ♀, which is the largest specimen, has a total length of 65 mm (incl. the rostrum). The smallest adult female is 55 mm long. The largest male is 63 mm, the smallest 57 mm long.

Description of male.

The male differs from the female in the following respects:

The abdomen is almost entirely symmetrical, both in dorsal and ventral view (Fig. 6b).

The first pleopods (Fig. 6c) are probably unique in being 1-jointed only. In the other genera in which the males have paired pleopods on the first abdominal segment they have two almost equally long joints (e. g. in *Tomopaguroides* Balss, 1912, fig. 15), whereas their shape is not mentioned in *Tomopagurus* A. M.-Edw. & Bouvier. Also the genera with paired pleopods 1 in females *(Pagurodes, Nematopagurus, Pylopagurus, Pylopaguropsis* and *Ceratopagurus)* have always 2-jointed first pleopods. In *Probeebei* they are furthermore small, less than half as long as the eye stalks, and with the distal half of the inner side slightly excavated. There is a double row of long setae along the posterior margin. – As mentioned above, faint scars of the absent pleopods 2-5 are visible on the small, triangular sternites (Fig. 6b).

The abdomen of a moderately berried female was dissected. The ovary was found to extend into the abdomen. It could not be stated whether a branch of the liver was also present, but it seems unlikely. A male was also dissected, and a pillow-shaped, whitish organ situated immediately inside the soft ventral skin might well be the testes, but the state of preservation was too poor to allow a detailed study. A similar organ was not found in the dissected female.

The gut of the male was filled with a black material. The only identifiable objects seem to be two fragments of tiny crustaceans.

Variation in adults.

The four adult females and three adult males were carefully compared, and besides the variation in size (see above) the following differences were found:

The rostrum is relatively shortest in the described ♀ in which it is a little less than one-fifth of the carapace (excl. of the rostrum), measured along the median line. The longest rostrum (another female) is a little less than one-third of this distance. In a third female it is bent horizontally at an angle of about 30°.

The number of spines on the carapace is somewhat larger in one male and two females which have e. g. a band of irregularly arranged spines along the median line of the posterior portion of the carapace – instead of one row in the described ♀ (Fig. 1).

The telson may have the hind corners considerably more rounded so that its shape is nearly oval instead of rectangular (Fig. 2c). There may also be setae along the entire hind margin.

The uropods show a slight variation in the width and length of the first joint compared to the length of the exo- and endopodites.

Post-larval development

No larval stages of this species were secured, but a number of juvenile specimens is available, including the holotype. They differ from the adults in having (1) the rostrum much more curved upwards distally (Fig. 2b, p. 14) and considerably longer (if stretched it would be half the length of the carapace (excl. of the rostrum); (2) the distal end of the telson is bent backwards in the youngest stage (cf. the description of the holotype); (3) the hairs on the carapace are longer; (4) the number of joints in the flagellum of the antennula and the antenna is smaller (cf. the description of the holotype); (5) in particular, in the younger stages the number of pleopods present in both sexes is remarkably different from that of the adult males and females.

In the Paguridae pleopods 2-5 (or 2-4) appear as bilobed formations generally in the fourth zoeal stage (metazoea) which is perfectly symmetrical.[1] In the postzoeal or glaucothoe stage (the fifth) the pleopods are also symmetrical and consist of a peduncle and two rami of which the outer one has long swimming setae. Already during this stage some of the intestines become wholly or in part abdominal, and the pleopods of the right side start degenerating. This procedure is independent of whether a shell is meanwhile occupied or not.

The first adolescent or. post-larval stage (or the sixth stage) is characterized by a completely asymmetrical abdomen like that of the adult. Generally the right hand pleopods disappear totally, although rudiments of these are visible on HART's fig. 118 (1937) of an adolescent crab of *Orthopagurus schmitti*, and THOMPSON (1903, p. 189) showed that under normal conditions (in the laboratory) 20 per cent of 107 specimens of *Pagurus annulipes* in the first post-larval (or sixth) stage retained rudiments of the right pleopods. But if he kept crabs of the glaucothoe stage without shell (naked), the average time of metamorphosis was not only postponed one or two days, but as much as 47 per cent (of 221 specimens) had retained rudimentary pleopods on the right side after the moult. In another experiment THOMPSON tried to rear such variants to the adult form. Due to a high mortality only 37 survived, and in no case did any crab preserve the variations beyond the second post-larval (or seventh) stage, and only 16 per cent retained them into that stage. That is, "whenever the moult from the sixth stage failed to give the normal adult pleopod formula, the succeeding ecdysis produced it" (l.c., p. 191).

In other respects juvenile characters are preserved for a considerable time through the first post-larval stages. In *P. annulipes* the full adult colours and the complete specific form are not attained until about the twentieth day from the glaucothoe, and the 9-jointed antennal flagellum of the sixth stage persists till the eighth stage, while crabs forty days from the glaucothoe have only 17 or 27 joints (THOMPSON 1903, p. 158).

Furthermore, FOREST (1954b) has reported on the first three post-larval stages of *Dardanus pectinatus* (Ortmann) and shown that in the first post-larval (or sixth) stage the right pleopods are almost as long as the left, although rudimentary in appearance (l.c., fig. 1A); in the next (seventh) stage they are tiny and bud-like, and in the eighth almost invisible knobs. In this stage the body is 6-7 mm long, whereas the body length of the adult is 23 mm (♂) and 37 mm (♀) (FOREST 1955, p. 100) so that probably several additional post-larval stages are found.

It was therefore surprising to find in the juveniles of *Probeebei mirabilis* that the right hand pleopods were still present in well-sized specimens which, apart from the longer and more upwards curved rostrum and a somewhat reduced number of joints in the flagellum, had attained all the characters of the adult. Three different stages besides the adults can be recognized. Judging from the relatively small increase in size (19-25-35 mm) they probably follow immediately after each other, but it seems likely that another, still unknown stage is found between the largest juvenile stage and the adults, in view of the considerable difference in size between them (35-37 mm and 55-65 mm).

Stage x. Three equally large specimens, 19 mm long, are found, but of one only the carapace is left and one lacks the abdomen. The sex of the third specimen is indeterminable, but it may be a

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[1] A tendency to asymmetry already in this stage may be found occasionally; MACDONALD *et al.* record e.g. (1957, p. 240) that the left of the bud-like pleopods 5 in stage IV of *Anapagurus laevis* is the larger.

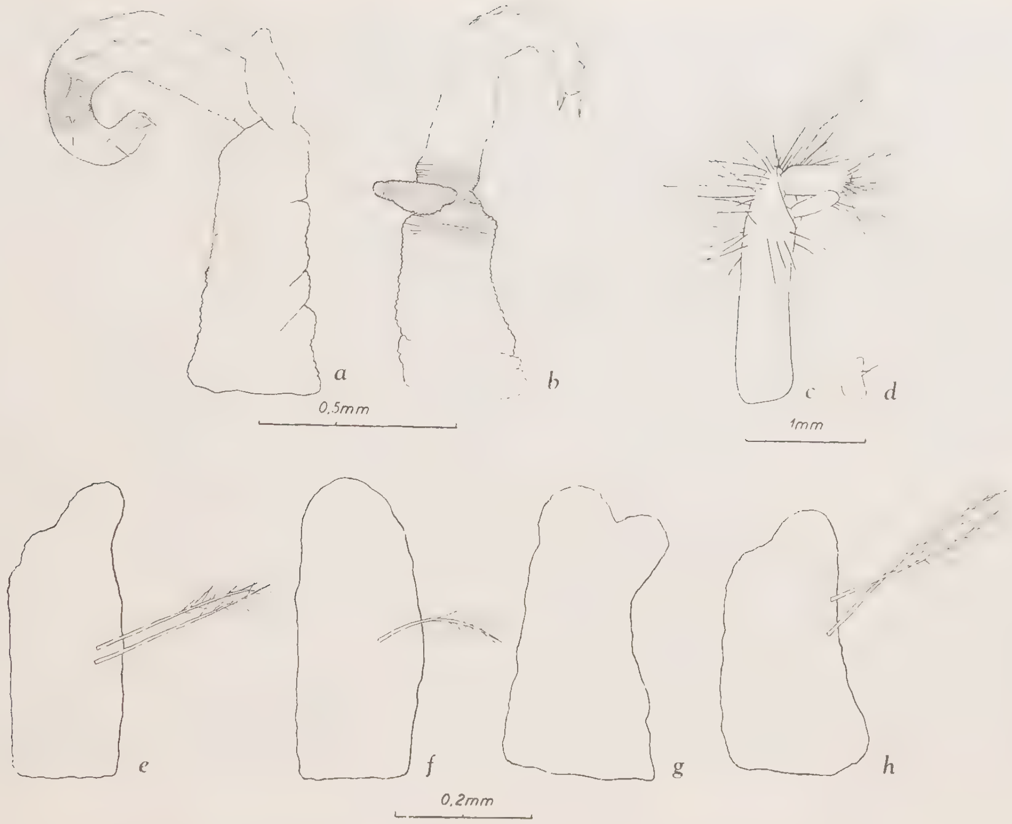

Fig. 8. *Probeebei mirabilis;* pleopods of developmental stages; a-b, left and right pleopod 2 of a ♀ of stage x; c, left plp. 2 of a ♀ of stage y; d and h, right plp. 2 of the same ♀; e-g, right plp. 2, right plp. 3 and left plp. 5 of a ♂ of stage y.

female because of the slightly larger rudimentary pleopods on the left side (see below). There is no trace of pleopods on segment 1. On both sides of the following four segments are rather large, although rudimentary pleopods (Fig. 8a-b). They are about 1.7 and 1.2 mm long, the left ones being slightly larger than the right. They consist of a peduncle, a small, unarmed endopodite and a much longer, curled exopodite with a row of tiny, peculiarly shaped spines towards the distal end. The entire surface is wrinkled with numerous very small folds. Thus, the appendages of this stage have a close resemblance with the *right* pleopods of the first post-larval stage of *Dardanus pectinatus* (FOREST 1954, fig. 1A), but not with the left ones which are without wrinkled surface and have long setae on the exopodite.

Stage y. All four specimens are 25 mm long. In the two females available the left pleopods 2-5 are further developed (Fig. 8c), on the whole differing from that of the adult (Fig. 6a) only in the relatively shorter rami and the less abundant equipment with setae. The right pleopods in the females and the right and left pleopods in the two males available are all very small (0.4 mm long) and bud-like (Fig. 8d-h); some of them may be faintly bilobed (8g). They may have one or two plumose setae, but these are occasionally absent.

Stage z. The two females available are 35 mm and 37 mm long. The left pleopods 2-5 are now fully developed, although of course smaller than in the adult. The right pleopods have disappeared, but, as in the adult, scars are distinctly visible. The sex opening is still closed. The appearance of the pleopods in juveniles and adults is summarized in table 1.

The holotype
(Figs. 9-10)

Material:

Arcturus Oceanographic Expedition St. 74-OT4, 60 miles S. of Cocos Island (4°50′N, 87°00′W), 1145 m, 30 May 1925. Gear: otter trawl. Bottom temp.: about 4,3°C.[1] – 1 juvenile ?female.

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[1] According to BEEBE (1926, p. 25) the temperatures at the only deep hydrographical station during the *Arcturus* Expedition (St. 50, 2°00′S, 89°30′W) is as follows: 1000 m depth: 4,8°C; 1500 m: 3,17°C. which by interpolation gives 4,3°C. at 1145 m. THOMSEN (1937, p. 11) records for

Table 1. Appearance of the pleopods in juveniles and adults of *Probeebei mirabilis.* 0 = no trace; Sc = scar of disappeared pleopod; Ru÷ = small rudiment, 0.4 mm long; Ru+ = large rudiment, 1.2-1.7 mm long; Pl÷ = almost fully developed pleopod; Pl = fully developed pleopod.

Abd. segment	Stage x Length: 19 mm		Stage y Length: 25 mm				Stage z Length: 35-37 mm		Adult Lenght: 55-65 mm			
	?Female		Female		Male		Female		Female		Male	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
1	0	0	0	0	0	0	0	0	0	0	Pl	Pl
2	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc
3	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc
4	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc
5	Ru+	Ru+	Pl÷	Ru÷	Ru÷	Ru÷	Pl	Sc	Pl	Sc	Sc	Sc

Comparison with *Galathea* specimens.

I am much obliged to Dr. Jocelyn Crane and to the New York Zoological Society for the generous loan of the holotype which enabled me to state with certainty not only the systematic position of this specimen, but also its identity with the *Galathea* specimens.

The holotype is a juvenile ?female and belongs to the above described stage x of which the *Galathea* collected three specimens. A careful comparison revealed an extraordinary similarity in all respects,[1] except the following three:

(1) The total length is 20,6 mm (as against 19 mm) because the carapace is more elongated (Fig. 9), being 1,35 times longer than broad (excl. of the rostrum), but only 1,29 times longer than broad in the *Galathea* specimens. (2) The rostrum is broken before the apex (Fig. 9), but probably did not bend so much backward as in the others (Fig. 2b, p. 14); it also lacks the dorsal spines near the base, of which the three *Galathea* specimens have three (Fig. 2b) and four and four. (3) On pleopods 2-5 the endopodites are still smaller than in the other specimens (Fig. 8a-b), being only about half as large.

Additional description.

The relatively longer and more curved rostrum and the more abundant growth of hairs on the carapace in comparison with that of the adults, as well as the shape of the pleopods were described above. Besides, the holotype and three *Galathea* specimens of stage x differ from the adults in the following features:

(1) The telson has the distal third bent backward in a peculiar way and rounded apically, when seen from behind (Fig. 10a). However, on the upper margin close to the apex two very small, soft, finger-shaped projections emerge, both of which point inward (towards the median line) where they meet (Fig. 10b-c). (2) There are 14 joints in the upper (outer) flagellum of the antennula, 5 in the lower; the flagellum of the antenna has about 70 joints.

Previous description.

The new genus and species was first mentioned in the paper in which Boone (1926 a) gave an enthusiastic account of the more unusual of the crustaceans from the *Arcturus* Expedition. She claimed (p. 72) that this "shy, small creature" was "the Missing Link", and discussed its systematic position. She rejected it as an aberrant amphipod because of the stalked eyes and macruran-like carapace. The large second abdominal segment reminded her of that of a lithodid crab, but, unfortunately, she abandonned the supposition that it belonged to the Anomura and ended with regarding the animal as a primitive macruran crustacean, although, as she said, it has "the carapace composed of seven *articulated* plates". This misconception is of course due to the fact that she included the six abdominal segments with the carapace.

In the second paper (1926 b) she gave a reasonably good illustration[1] of the animal in side view

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Dana St. 3556 (2°52′N, 87°38′W), which is very close to *Arcturus* St. 74, at 1000 m: 4,66°C. and at 1200 m: 4,20°; this again points to a temperature of 4,3°C. at 1145 m depth.

[1] Even the armament with spines is more equal in the holotype and in one of the *Galathea* specimens, than in the three *Galathea* specimens mutually.

[1] Apart from minor inaccuracies (e.g. exaggerated length of the dactylus of peraeopod IV) the abdomen has had an extra segment included between segments 5 and 6, and

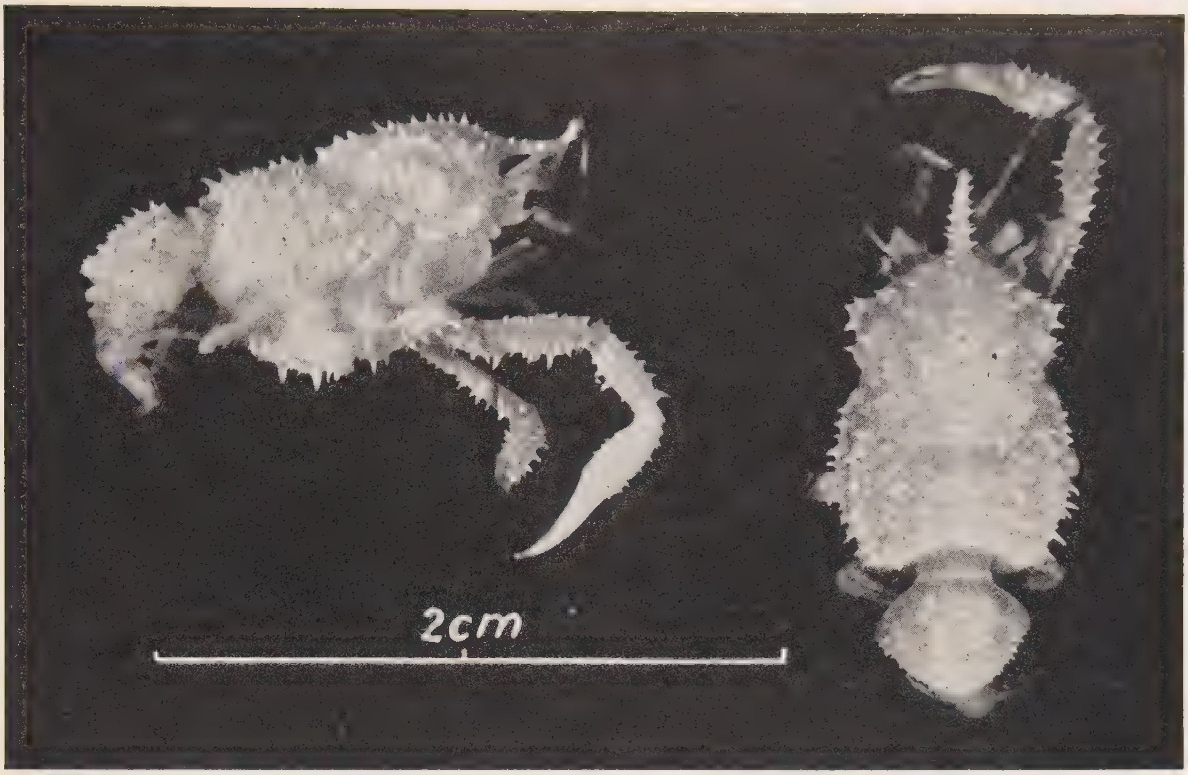

Fig. 9. *Probeebei mirabilis;* holotype.

and the following description (the numbers in brackets refer to the comments given below):

"(1) Family: PROBEEBEIDAE.

Rostrum well developed. (2) Carapace consisting of seven articulated segments. (3) First legs equal, strong, chelate. Outer antennae with scapocerite; flagellum very long. Second antennae long, multiarticulate, biflagellate. Second abdominal segment arched, armoured as the carapace. Rhipidura flexible. Telson transversely divided, distal section reflexed rigidly upon proximal half.

Genus: *Probeebei,* with characters of family. Only genus known. Type: *Probeebei mirabilis* new species.

Probeebei mirabilis, sp. nov.

(4) Rostrum half as long as carapace, upturned. Carapace consisting of seven articulated plates. Eyes prominent. First abdominal segment hingelike, second very prominent, arched. Rostrum, carapace and first two abdominal segments ornamented with rows of prominent spines; (5) third to sixth segments inclusive smooth, subcylindrical, deflected; (6) second, third and fourth segments with degenerate uniramous pleopoda attached at outer lateral margin, resembling side plates. Rhipidura slender, sublunate, outer blade larger. (7) Telson small, transversely segmented, apical part rigidly deflected upon proximal half, tip hooklike, upturned. First legs chelate symmetrical, second and third broken, basal parts are replica of first pair. Third and fourth legs weak. (8) Mouthparts unique."

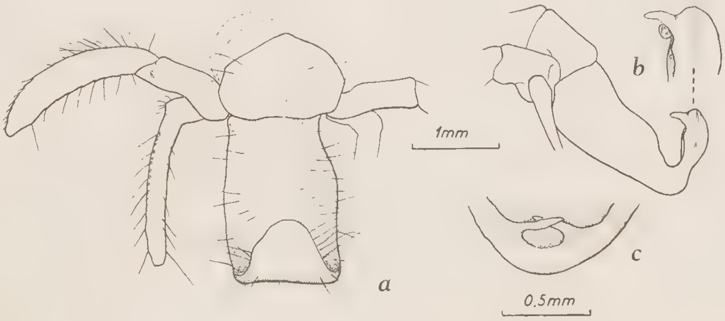

Fig. 10. *Probeebei mirabilis,* holotype; a, abdominal segment 6 and telson from behind; b, the same from the left side; c, the distal part of the backward bent section of telson seen apically.

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the pleopods on segment 5 have been left out. According to the illustration both chelipeds were previously present, but later the left chela has been lost.

Comments.

(1) For the reasons given below (p. 26) the family will have to be rejected.

(2) As stated above, this is definitely not the case.

(3) Also in this developmental stage the right cheliped is slightly larger than the left. This is also evident from BOONE's illustration.

(4) Rostrum is half as long as the anterior portion of carapace.

(5) Abdominal segment 3 has a transverse row of many small spines or knobs along the posterior margin and segment 4 a few tiny knobs.

(6) Also segment 5 has pleopods; all pleopods are biramous, but the endopodites are very small and easily overlooked.

(7) Telson is not transversely segmented.

(8) The above description of the mouthparts of the adult shows that they are typically paguridean. They were not dissected by BOONE.

Phylogenetically significant relationships

MELIN (1939, p. 13) pointed out that in the systematic classification of the Paguridae more stress is laid on characters which facilitate a quick identification of the genera than on those which are of real importance for the systematics and phylogeny of the family. Naturally, it is tempting, in a group like hermit crabs which exhibits such a variety of life habits and biological adaptations, to lay too much stress on those characters which are a result of their adjustment to the environment, because they are so easily discernible. The true relationship of the genera should not be based on such easily adaptable and secondary characters, but on those which are not altered by the mode of life and the environment, thus being of a much more conservative nature.

Accordingly, I have tried to base the following considerations on the relationship of *Probeebei* entirely on the latter type, and in the following chapter I shall discuss the other characters of little or no phylogenetic importance.

MELIN (l. c., p. 16) emphasizes the great systematic significance of the number of pleopods which has been so greatly reduced during the evolution of the Paguridea. This character was already pointed out by BOAS (1924, p. 29) who based a new subdivision of "Paguriden" (including the Pylochelidae) on the number of pleopods present. His classification is the following:

1. Pylochelinen: Paired pleopods on abdominal segments 1-6.

2. Paguristinen: Males with a pair of pleopods on the first, sometimes also on the second segment.

3. Pagurinen (including Coenobitidae): Males without paired pleopods; first abdominal segment free, not fused with the last thoracic segment; terga on abdominal segments in one piece; 14 pairs of gills; no spine on joint 3 (ischium) of mxp. 3.

4. Eupagurinen: Males without paired pleopods; first abd. segment free; terga on abd. segments 2-5 paired; 11 pairs of gills; a spine present on joint 3 of mxp. 3 proximal to the *crista dentata*.

Thus, BOAS entirely rejects the ordinary division into Pylochelidae (with paired pleopods on segments 1-6), Paguridae (the flagellum of the antennula pointed; the peduncle rarely as long as the carapace), and Coenobitidae (the flagellum ends bluntly; the peduncle as long as or longer than the carapace). Also the long established division of the Paguridae into Diogeninae Ortm. (= Pagurinae Ortm.) and Pagurinae Latr. (= Eupagurinae Ortm.) by means of the width of the sternum between the third maxillipeds is disregarded.

Unfortunately, MELIN (1939) does not at all refer to the said paper by BOAS which he probably did not know.[1] This is so much more regrettable, since MELIN (p. 14) – in my opinion rightly – chritizises the somewhat arbitrary character (distance between the bases of the third maxillipeds) by means of which the two subfamilies of the Paguridae are divided. Although he bases his excellent key to the genera of this family primarily on the number of pleopods in both sexes, he prefers to retain the old subdivision. This has also been done by all later authors (e. g. FOREST 1955, FIZE & SERÈNE 1955, and BALSS 1957a). It is beyond the scope of this paper to enter into a detailed discussion of this problem, but I feel convinced that the present, generally accepted classification of the hermit crabs cannot be regarded as the phylogenetically most satisfactory one.

According to BOAS' system *Probeebei* falls within the Paguristinen, since in the males a pair of pleopods is present on the first segment. BOAS divided this subfamily as follows:

(1) Also the female with one pair of pleopods on the first segment; 13-14 pairs of gills: *Paguristes, Munidopagurus, Paguropsis.*

(2) Female without pleopods on the first segment:

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[1] MELIN's paper was edited posthumously by BALSS who very regrettably did not include a list of references.

Xylopagurus, Parapagurus, Sympagurus,[1] *Tomopagurus, Tylaspis.*

Of these, *Munidopagurus* can only be included with considerable doubt, since only one female of the monotypic *M. macrocheles* (A. M.-Edw.) is known (MILNE-EDWARDS & BOUVIER 1893, p. 102), so that nothing can be said of the male pleopods.[2] Moreover, BOAS forgot to include *Tomopaguropsis* Alcock, 1905 and *Tomopaguroides* Balss, 1912, in which the male has one pair of pleopods. Accordingly, a subdivision can be made as follows (with the number of unpaired pleopods in brackets):

(1) Male with two pairs of pleopods, female with one:
Paguropsis Henderson (♂ 3, ♀ 4)
Paguristes Dana (♂ 3, ♀ 4)
[? *Munidopagurus* A. M.-Edw. & Bouv (♂ ?, ♀ 3)]
(2) Male with two pairs of pleopods, female without paired pleopods:
Xylopagurus A. M.-Edw. (♂ 0, ♀ ?)
Parapagurus Smith (♂ 3, ♀ 4)
Sympagurus Smith (♂ 3, ♀ 4)
Tylaspis Henderson (♂ 3, ♀ ?)[3]
(3) Male with one pair of pleopods, female without paired pleopods:[4]
Tomopaguropsis Alcock (♂ 4, ♀ ?)
Tomopaguroides Balss (♂ 3, ♀ ?)[3]
Tomopagurus A. M.-Edw. & Bouv. (♂ 3, ♀ ?)[3]
Probeebei Boone (♂ 0, ♀ 4)

Paguropsis and *Paguristes* also differ by having the third maxillipeds close together and therefore belong to the subfamily Diogeninae while all the other genera can be referred to the Pagurinae.

MELIN (l. c.) has also evaluated the systematic importance of the number and type of gills in the Paguridae and considers the number to be very significant, because of its bearing on the phylogeny. On the other hand, the significance of the type of the gills – whether tricho- or phyllobranchiae – has previously been much overestimated. He shows very convincingly that the former cannot be homologonized with the trichobranchiae of the Macrura from which the Paguridea have descended. They must in this group probably always be looked upon as phyllobranchiae which secondarily have been split up longitudinally so that they have four branches instead of two.

According to number and type of gills, the genera in question can be arranged in the following way (the gills of *Tylaspis* are unknown):

(1) With 13 pairs:
Tomopaguroides (trichobr.)
Paguropsis (phyllobr., bifid)
Tomopaguropsis (phyllobr., bifid)
Paguristes (phyllobr.)
Xylopagurus (phyllobr.)
[? *Munidopagurus* (phyllobr.)]
(2) With 11 pairs:
Parapagurus (trichobr.)
Sympagurus (phyllobr.)
Tomopagurus (phyllobr.)
Probeebei (phyllobr.)

Probeebei has a very small flagellum (appendix) on the endopodite of the maxillula (Fig. 3 b, pag. 16). In most of the above mentioned genera this appendage is not described. The flagellum is absent in *Parapagurus, Xylopagurus,* and *Tomopagurus*. It is well developed (2-jointed) in *Paguristes*.

MELIN does not mention the significance of the presence or absence of a flagellum on the exopodite of the first maxillipeds, but in my opinion this must be at least as important as the flagellum of the maxillula. In the above genera it seems to be absent only in *Parapagurus, Sympagurus* and *Probeebei* and is at any rate present in *Paguristes, Xylopagurus, Tomopaguropsis,* and *Tomopagurus*.

Finally, after correctly having denied the morphology of the very adaptable chelipeds any systematic importance, MELIN (l. c.) claims that besides the heterochirality also the plane in which the fingers move is of "rather great systematic value". I have compared two extremes, *Parapagurus* and *Pagurus* (= *Eupagurus)* and found this character so arbitrary that in my opinion little importance should be attached to it. Anyhow, in *Probeebei* the movement is very much as in *Pagurus* and must therefore be in the horizontal plane.

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[1] This genus is now generally regarded as a synonym of *Parapagurus*.

[2] It is more likely that *Munidopagurus* should be ranged with the following genera, the females of which have also one pair of pleopods while the males have exclusively unpaired pleopods: *Pylopaguropsis, Pylopagurus, Pagurodes, Nematopagurus,* and *Ceratopagurus*.

[3] The females of *Tylaspis, Tomopaguroides* and *Tomopagurus* are unknown.

[4] FOREST (1952, p. 8, fig. 8) has described and figured a strange irregularity occurring in *Trizopagurus strigimanus* (White) which belongs to the Diogeninae: Besides the normal left pleopod 2 the males always have also the right second pleopod developed, but it is smaller and with a greater variation in the shape of the exopodite.

If we primarily consider the number of paired pleopods and of gills, we find that *Probeebei* is closest related to *Tomopaguropsis*, *Tomopaguroides* and first and foremost to *Tomopagurus;* with the latter it does not only agree in number of paired pleopods and in number and type of gills, but also in the horizontal movement of the fingers of the chelipeds.

It differs from *Tomopagurus* in having no unpaired pleopods in the male, in the presence of a small flagellum on the maxillula and the absence of a flagellum on the first maxilliped.

It also agrees with *Parapagurus* (and *Sympagurus)* in several respects: Number of gills, absence of flagellum on the first maxilliped, and lack of right genital opening in the female (see below). It differs in number of male pleopods and presence of a small flagellum on the maxillula.

It is interesting that all the genera listed below, which are most closely related to the bathyal-abyssal *Probeebei* are sublittoral or preferably bathyal or abyssal, thus very rarely occurring at temperatures above 15° C. or there-about.

Tomopagurus rubropunctatus: Barbados, 132 m.
Tomopaguropsis lanata: Off Ceylon, 260-730 m and 668 m.
Tomopaguropsis problematicus: Off Florida and Barbados, 229 and 527 m.
Tomopaguroides valdiviae: Off East Africa, 1079 m.
Xylopagurus rectus: West Indies, 245-267 m.
Xylopagurus cancellarius: Off Colombia, 73 m.
Tylaspis anomala: Central South Pacific, 4343 m.
Parapagurus (about 10 species): Cosmopolitan, bathyal and abyssal (to 4130 m), except two littoral species (18 and 35 m) at high latitudes.
Sympagurus (about 10 species): probably cosmopolitan, bathyal, except one sublittoral species (S. E. Australia, 40-102 m).

Generically, *Probeebei* is well characterized by the calcified abdomen, the presence of a small flagellum on the endopodite of the maxillula, the lack of a flagellum on the exopodite of the first maxilliped, the number of pleopods, and the number and type of gills. However, as demonstrated above, it falls well within the frames of existing families and subfamilies. Consequently, the family Probeebeidae (BOONE 1926 b) must be rejected.

Similarities by convergence

Shape and calcification of the carapace and the abdomen. BORRADAILE (1916) pointed out that Nature's attempts to evolve a crab by convergence result in forms with broadened, mostly flattened carapaces, preferably with spines along the margins and with a distinct rostrum. The abdomen becomes reduced and is eventually bent firmly under the thorax in the way found in Lithodidae, *Lomis,* Porcellanidae, and in true crabs. Less carcinized hermit crabs than *Lomis* and the Lithodidae are the following pagurid genera (Fig. 11): *Porcellanopagurus* (with four Pacific species which hide the short, almost symmetrical abdomen under a bivalve shell), *Tylaspis* (with one Central Pacific, abyssal species with somewhat reduced, probably uncovered abdomen), *Ostraconotus* (with one West Atlantic species with much reduced, uncovered abdomen), and, finally, the Robber Crab *Birgus latro* with a large, almost entirely calcified abdomen. A further example is *Probeebei*. All these five genera have the posterior portion of the carapace larger and more swollen than in the ordinary hermit crabs in gastropod shells. This portion is also as calcified as the anterior one, except in *Porcellanopagurus* where it is covered by the bivalve shell. A distinct rostrum is present in all except *Ostraconotus*. A depression of the carapace similar to that in especially *Porcellanopagurus* and *Ostraconotus* is not found in *Probeebei*.

BORRADAILE (l. c.) already called attention to the extraordinary similarity in shape and calcification of the carapace between the above genera and the N. E. Pacific, littoral species *Pagurus splendescens* (Owen) which also exhibits the same grooves as *Probeebei* (p. 14). However, its abdomen appears to be just as soft and asymmetrical as in other species of *Pagurus* and to be hidden in a snail shell. It seems difficult to understand what has induced this marked carcinization of the thorax in *P. splendescens*. A close study of the morphology and habits of the species might throw light on this point, but, unfortunately, no specimens were available to me.

The abdomen of *Probeebei* is more calcified than in any other representative of the Paguridea, except the Lithodidae and *Lomis*. It is soft-skinned in *Porcellanopagurus*, *Tylaspis* and *Ostraconotus,* but almost fully calcified in the symmetrical Pylochelidae and in *Birgus*. In the latter the great majority of the outer surface of each abdominal segment is covered by the large, flat tergum and by "small subsidiary platelets (pleura) on either flank" (ALCOCK 1905, p. 149) – cf. HARMS 1932, pl. 8-10. In *Probeebei* the terga not only cover the entire outer surface of the segments, but are also sculptured and furnished

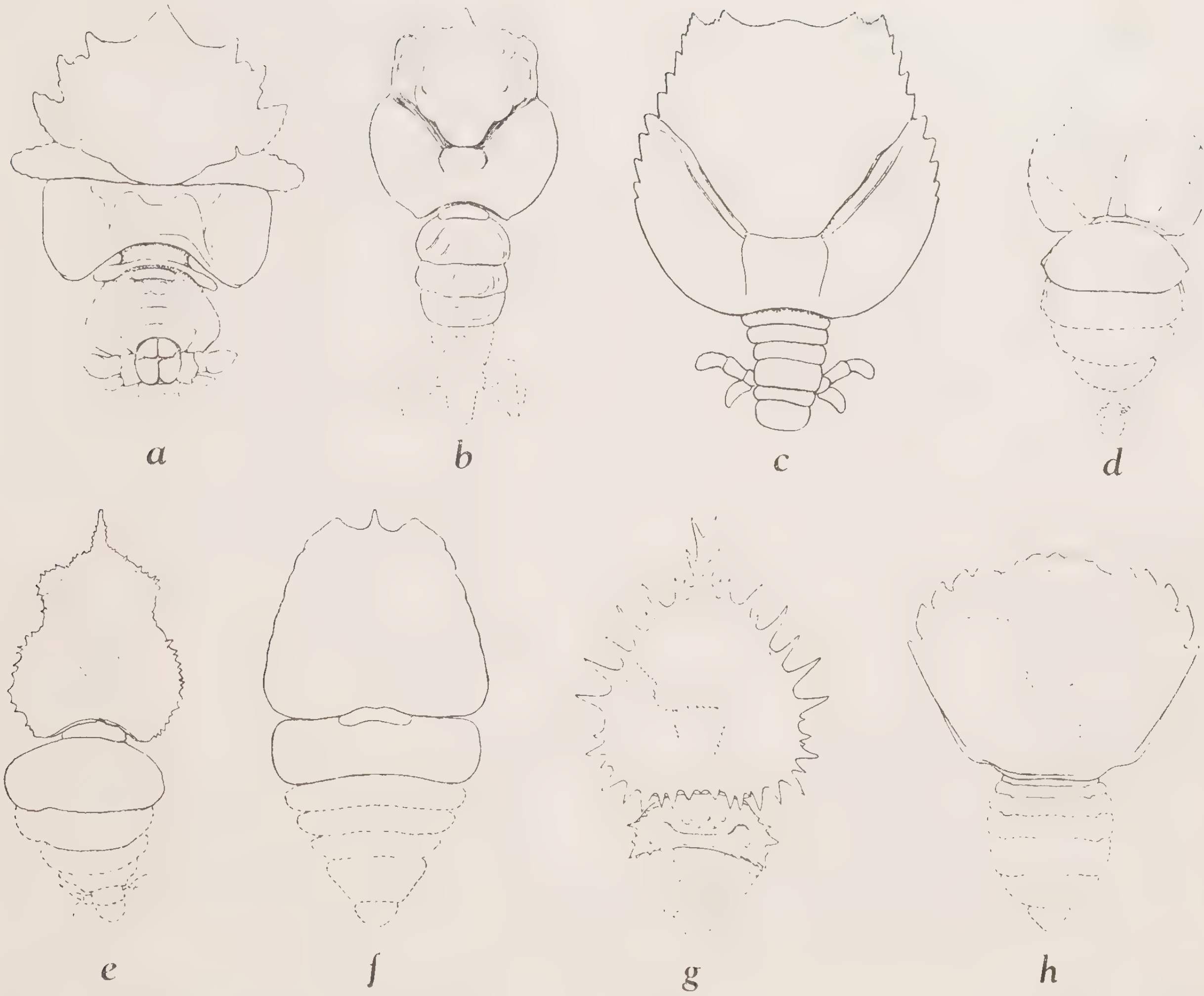

Fig. 11. Carcinization in Paguridea. In each case the part indicated by a dotted line is normally carried under the rest of the body. Not drawn to scale. a, *Porcellanopagurus;* b, *Tylaspis;* c, *Ostraconotus;* d, *Birgus;* e, *Probeebei;* f, *Lomis;* g, *Lithodes;* h, *Carcinus.* (After Borradaile 1916, somewhat altered).

with a stabilizing crest along the posterior margin. As in *Lithodes arctica* the second segment is much larger than the others and consists of a single plate without sutures. – A symmetrical or practically symmetrical tail-fan is found not only in the above mentioned genera, but also in species which hide the abdomen in a straight and elongated cavity, e. g. in wood *(Xylopagurus)*, in a *Dentalium* shell *(Tomopaguroides*, species of *Parapagurus* and *Pylopagurus)*, in straight annelid tubes *(Orthopaguropsis*, species of *Pylopagurus)*, in a sack-shaped *Epizoanthus* colony *(Paguropsis)*, or in coral rock *(Cancellus)*.

Unpaired sexual opening in the female. In females of *Probeebei* only the *left* genital opening on the coxa of peraeopods III is developed – without any trace of the corresponding opening on the right coxa. This peculiar feature was previously described in a few other genera only: *Parapagurus* (and *Sympagurus)* and *Paguristes;* in the latter it is restricted to nine littoral species along the West-African coast and one species in the Red Sea (Forest 1954 a, p. 160 and fig. 69). Thus, the unpaired left pleopod is found only in genera in which there are one or two pairs of pleopods in the males. Of the remaining of such genera the openings are paired in all the species of *Paguropsis* which are kept in this Museum. On my request females of the following species were kindly examined by the following colleagues: *Xylopagurus rectus* (A. M.-Edw.) by Dr. J. Forest (Paris), *Tomopaguropsis problematicus* (A. M.-Edw. & Bouvier) by Dr. E. Deichmann (Harvard), and *T. lanata* Alcock by Dr. G. Ramakrishna (Calcutta); in all cases the genital openings were found to be paired. Females of the remaining genera *(Tomopagurus, Tomopaguroides*, and *Tylaspis)* are unknown.

In females of one species of the Pylochelidae, *Cheiroplatea laticauda* Boas, the opposite is found: the *right* genital opening is present, the left absent. I found the similar in an unidentified species of *Diogenes* in this Museum, and Dr. Forest kindly informed me that this is also the case in three species of *Diogenes: D. custos* (F.), *D. miles* (Herbst), and *D. diogenes* (Herbst).

Apparently, it is not possible to ascribe any phylogenetical significance to unpaired female genital openings. Although a left opening occurs exclusively in genera with paired male pleopods, this is not the case in all such genera, and in *Paguristes* it is found only in some of the species; moreover, the genera belong to two different subfamilies. Genera with an unpaired right genital opening *(Cheiroplatea* and *Diogenes)* are still less related, and also in *Diogenes* only some species exhibit this feature.

Appendages. The ocular peduncles and corneae of *Probeebei* do not show any reduction despite the abyssal environment. The opththalmic scale is, however, unusually small and is apparently absent in the likewise abyssal *Tylaspis anomala* (Henderson 1888, p. 81). Both species have also a low number of joints (six) in the lower flagellum of the antennula and peraeopods II and III are considerably elongated (especially the dactylus) and somewhat compressed. This feature is found also in species of the bathyal-abyssal genus *Parapagurus,* and a similar elongation of the walking legs is well known in a great many deep-sea crustaceans. Peraeopods IV of *Probeebei* have lost the function of being pressed against the inner wall of the gastropod shell and of assisting in the movement out of and into a shell (Brock 1926, p. 437); accordingly, they are without file-like surface and – again as in *Tylaspis* (Borradaile 1916, fig. 12) – with a rudimentary chela which cannot function as such. The abundant growth of soft setae, also on this pair of legs, may indicate that they share with peraeopods V the cleaning of the gill chamber and perhaps also of the eggs. Finally, also the outer surface of the uropods has become almost smooth, not file-like.

Conclusions

No other group of crustaceans exhibits such a variety of adaptations to the environment as the hermit crabs. The primitive, still entirely symmetrical Pylochelidae descend almost directly from halassinid ancestors and have primarily survived at bathyal depths where the possibilities of a partly hidden existance apparently are the best. The evolution of the Paguridae has undoubtedly taken place in shallow water in the tropics on a hard bottom of corals or rock where, however, the feasibility of digging retreats is small. Here the habit of hiding the semi-calcified, exposed abdomen first in natural cavities in the rock (Boas 1926 a, p. 8) and later in the ever abundant, empty gastropod shells evolved, and the asymmetry and other adaptations to life in a shell were eventually introduced. Harms (1932, p. 275) claims that the acquisition of the asymmetrical abdomen is not very old, since it is not yet perfectly genotypically induced: Marchal (1891), Bouvier (1892), Thompson (1903), and others report on pagurids which with equal readiness accept left coiled as well as the usual right coiled gastropod shells. Another example of this is probably found in *Paguropsis typica* Henderson which protects the almost symmetrical abdomen with a colony of the actinian *Epizoanthus paguropsidis.* Both Alcock (1905, p. 27) and Boas (1926 b, p. 14) report that in both sexes now the left, now the right pleopods are developed. On the other hand, the asymmetry of the hermit crabs is so genotypically fixed that it inevitably appears in the first post-larval stage, independent of whether a snail shell is occupied or not.

In places where gastropod shells were not available in sufficient number (or for other reasons?) the hermit crabs have had the ability to find other means of protecting their abdomen. The furthest advanced adaptation towards this challenge of the environment is undoubtedly found in the Lithodidae or Stone Crabs which are perfectly carcinized, but between this, probably very recent, group (which is unknown as fossils) and the typical, asymmetrical hermit crabs in gastropod shells we find a rich variety of transitional forms. It is characteristic that most of these are met with in the deep-sea, although some *(Cancellus, Orthopaguropsis, Xylopagurus cancellarius, Porcellanopagurus* a. o.) are littoral.

There are several examples of *Dentalium* shells being occupied by Paguridae in the deep-sea: *Parapagurus chuni, P. spinimanus, Tomopaguroides valdiviae* (Balss 1912, pls. VIII-XI) and *Pylopagurus discoïdalis* A. M.-Edw. (Milne-Edwards & Bouvier 1893, pl. VI, 7) have attained a totally symmetrical abdomen apart from the lack of right hand pleopods. All these species are bathyal.

A further step has been taken by the above mentioned species *Ostraconotus spatulipes* (A. M.-Edw.)

which lives at 220 m depth in the West Indies and *Tylaspis anomala* Henderson (1888, p. 81) which is the so far deepest recorded hermit crab from a depth of 4343 m in the Central South Pacific. *Tylaspis* has had the abdomen somewhat, *Ostraconotus* the abdomen greatly reduced (Fig. 11). There is no doubt that the abdomen is unprotected in the latter,[1] while the situation in *Tylaspis* is unsettled. HENDERSON and BORRADAILE who are the only ones who have actually studied the male holotype and only specimen both suggest some sort of protection. The former says (l. c.): "The form of the abdomen points to the species having occupied some other dwelling place than the Gastropod shell usually selected by the soft-tailed Pagurids", and BORRADAILE writes (1916, p. 123): "– the soft abdomen is probably somehow protected in life. Perhaps ... it is merely buried in the soft ooze of the sea floor. Certainly in *Ostraconotus* it is not carried under the cephalothorax, and its unarmoured dorsal side makes it unlikely that this is the case in *Tylaspis*." On the other hand, BALSS (1924, p. 763) and MELIN (1939, p. 15) take it for granted that *Tylaspis* lives freely. Without having seen the specimen it is of course difficult to decide this question, but at any rate it seems impossible – judging from the extreme length of the walking legs – to presume that the soft abdomen is buried in the ooze, as suggested by BORRADAILE. The similarity in general appearance with the undoubtedly free-living *Probeebei*, the lack of working chelae on peraeopods IV, and the very small size of these and prps. V[2] make it most probable that the abdomen is unprotected in spite of its soft-skinned nature.

The most advanced evolution along the said line has been achieved by *Probeebei mirabilis* with its fully calcified and well armoured carapace and abdomen. It is difficult to determine how many of the previously mentioned similarities between this species and *Tylaspis* are due to true relationship and how many to convergence in an equal environment, the more so since females of *Tylaspis* are unknown.

Among the asymmetrical pagurids there are three instances of forms with a fully calcified abdomen, viz. the Lithodidae, *Birgus latro* and *Probeebei*, which have arisen from very different stocks within the Paguridae: the Lithodidae from species of Pagurinae close to *Nematopagurus* and *Pylopagurus* of the present day (BOAS 1924, p. 25), *Birgus* (and *Coenobita)* from Diogeninae, and *Probeebei* from the primitive "Paguristinen" of BOAS (1924).

The Lithodidae represent the most advanced, almost crab-shaped stage, while *Birgus* and *Probeebei* are unable to fold the abdomen firmly against the thorax. It is interesting to observe that the two latter, apparently very parallel, lines of evolution have occurred in habitats which must both be considered extremes: dry land and the abyssal depths. It is also characteristic that the genus *Birgus* is definitely and *Probeebei* probably monotypical.

In *Birgus* the calcification of the abdomen is certainly a result of the fact that easy access to very nutritious fruits far inland has led to a giant growth and subsequent lack of sufficiently large shells for protection (HARMS 1932, p. 279). Unlike the species of the also land-dwelling genus *Coenobita* which may take advantage of very large shells of *Turbo*, the Robber Crab never makes use of marine shells (HARMS 1938, p. 21) and is thus restricted to the usually small-sized species of land shells on their native island.

HARMS could postpone the calcification of the abdomen and a considerable number of other characters related to a free-living habit (1938, p. 33) by experimentally offering the young crabs sufficiently large gastropod shells. On Christmas Island the crabs may give up the shell cover already in the first post-larval stages and must invariably do so after a few further moults, at a length of carapace of 6-7 mm. In the Moluccan Islands this occurs at a length of 10-11 mm, but four-year-old crabs from Christmas Island with a carapace length of 21 mm and a soft and perfectly asymmetrical abdomen, hidden in a shell, were still alive in captivity when HARMS' paper was published.

If the interpretation of these experiments is correct, they seem to indicate that the calcification of the abdomen of *Birgus* is not yet genetically fixed and suggests a relatively late evolution of the species. This is supported by the fact that no fossils of *Birgus* are known, in spite of its large size and well calcified exterior.

The recovery in the Lithodidae, *Birgus* and *Probeebei* of a calcified abdomen must, however, have taken place over a long period of time. PRZIBRAM (1907) claimed that experiments with species of *Pagurus* and *Diogenes* without a shell ("enthäust") showed that already after the first moult they would

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[1] Except BORRADAILE (1916, p. 123) who presumes that it may be buried in the soft sediments on the bottom.

[2] MELIN (l.c.) writes that prps. V are monodactylous, but HENDERSON only describes them as "almost rudimentary" without further explanation.

acquire a distinctly segmented, rather contracted abdomen with a somewhat hardened and pigmented skin. This result is in strong opposition to the findings of THOMPSON (1903): Quite independent of the presence or absence of a shell the young hermit crab will in the glaucothoe and the first of the post-larval stages acquire an asymmetrical abdomen into which certain intestines will move. Later BRINCKMANN (1926) repeated PRZIBRAM's experiments on a much larger scale and very convincingly showed that also in adult hermit crabs the morphology of the abdomen is not the least influenced by the removal of the shell.

Finally, it should be pointed out that in several respects *Birgus*, during the evolution to the habit of a freely roaming animal, has become considerably more changed than *Probeebei*. This cannot be explained by the fact that *Birgus* is restricted to dry land, which must be the most extreme habitat for decapods. A comparison with the closely related Coenobitidae which are also land-dwelling, but use a shell, shows that only *Birgus* has acquired the characters mentioned below.

In one essential respect, calcification of the abdomen, *Probeebei* is further advanced than *Birgus* (p. 26). On the other hand, peraeopod IV of *Probeebei* has still almost the same size as in shell-bearing pagurids, but when *Birgus* leaves the shell and becomes free-living this leg is modified from a short appendage used for holding the shell into a strong leg which, together with the preceding legs, is used for walking.[1] Besides, not only the male, but also the female abdomen of the adult *Birgus* is practically symmetrical, and the uropods have become reduced almost to nothing. Also the eye-stalks, the antennulae, and the antennae are different from those in Coenobitidae, and a pair of lungs is developed.

Probeebei mirabilis shows only one feature which is characteristic of many deep-sea decapods: the elongate walking legs. As in other abyssal pagurids, the eyes are apparently well developed (although the ophthalmic scale, as in *Tylaspis*, is reduced), the size of the eggs is very small, and the colour of the carapace and legs is unusually bright for a bathyal-abyssal animal.

Acknowledgments

My sincere thanks are due to Dr. FENNER A. CHACE of the U. S. National Museum for directing my attention to the description of *Probeebei mirabilis*, thereby giving me the fine opportunity to have this species pinned down. Also to Dr. JOCELYN CRANE and the New York Zoological Society for lending me the holotype without which the identity of the material could not have been established. Dr. JACQUES FOREST of the Natural History Museum in Paris furnished me with valuable information about unpaired sexual openings in female pagurids and with a photostat copy. The majority of the illustrations were prepared by Mr. POUL H. WINTHER.

Summary

1. *Probeebei mirabilis* Boone, 1926 is redescribed. It is primarily characterized by the completely calcified carapace and abdomen, the elongated peraeopods II and III, lack of paired pleopods in the female, presence of paired pleopods 1 in the male, and 11 pairs of phyllobranchiae. The abdomen is very nearly symmetrical in the male, asymmetrical in the female. The adults are 55 mm-65 mm long; they show only slight variation.

2. Three late post-larval stages are available. In view of their considerable size (19-25-37 mm) it is remarkable that the reduction of the right pleopods 2-5 in the female and left and right pleopods 2-5 in the male does not occur till during the youngest of these stages.

3. The holotype is a juvenile, belonging to the youngest of the post-larval stages represented in the *Galathea* material; practically no differences were found. The original description is cited and discussed.

4. The holotype was collected by the *Arcturus* Expedition S. of Cocos Island, Gulf of Panama at 1145 m depth and 4,3°C. The *Galathea* material comprises 18 specimens from the East Pacific off Costa Rica, 3570 m depth, 2,0°C.

5. Phylogenetically, *Probeebei* is most closely related to other genera with paired pleopods in the male and 11 phyllobranchiae: *Tomopagurus, Parapagurus* (and *Sympagurus)*, and *Tylaspis*. Of these the three last ones are also bathyal or abyssal in distribution.

6. *Probeebei* is another instance of carcinization, i. e. the evolution by convergence of crab-like forms which has occurred in several, systematically unrelated pagurids. Both in carcinized pagurids and in species which protect the abdomen in more or less straight objects such as *Dentalium* shells, worm tubes, pieces of wood, and coral rock, the abdomen has become secondarily symmetrical to a larger or

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[1] In the Lithodidae peraeopod IV has even become as large as and shaped exactly like the two preceding pairs of legs.

smaller degree. Such forms are primarily found at bathyal or abyssal depths where sufficient gastropod shell material apparently is not available. The most advanced step was taken by the Lithodidae, the Robber Crab *Birgus latro,* and *Probeebei* which all have a completely calcified, unprotected abdomen. The former and the latter evolved in cold waters, while *Birgus* became a terrestrial form. The evolution of *Birgus* and *Probeebei,* which are only distantly related, has taken place along parallel lines. The abdomen of *Probeebei* is more thoroughly calcified, but in other respects (use also of peraeopods IV as walking legs, almost complete reduction of the uropods, more symmetrical abdomen in the females, etc.) *Birgus* is more adapted to the life as a freely roaming animal.

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THE PORCELLANASTERIDAE

A MONOGRAPHIC REVISION OF AN ABYSSAL GROUP OF SEA-STARS

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PREFACE

The Porcellanasteridae s. str. form within the Asteroidea a well circumscribed group the members of which are easily distinguished from all other sea-stars by the presence – in each interbrachial angle – of one or more of the so-called cribriform organs. The group is further distinguished biologically by being exclusively confined to the deep-sea. So far no porcellanasterids have been found in depths less than about 1000 meters, and more than half of the records are from depths exceeding 3000 m.

The present paper reports on the large material of porcellanasterids brought back by the Danish Deep-Sea Expedition on the 'Galathea' in 1950-52, and on a few specimens taken in 1920 by the 'Pickle' of the South African Fishery Investigations. Further the paper summarizes and discusses all which is previously recorded concerning the porcellanasterids.

The study is essentially morphological and taxonomical, but at the same time it forms the main basis of the following paper in this report: On the zoogeography and origin of the abyssal fauna in view of the knowledge of the Porcellanasteridae.

The text-figures illustrating structural details were drawn by means of a camera lucida, but are sometimes slightly diagrammatic; no attention has been paid to the ornamentation of the skeletal elements, and occasionally, in case of defect specimens, the illustrations of the spine-armature have been combined from different plates and ossicles. The author's English was revised by Mrs. A. Volsøe.

INTRODUCTION

Historical review (expeditions and authors)

The porcellanasterid sea-stars were completely unknown to science until 1873 when they were brought to light during the early part of the first great deep-sea expedition, the famous voyage of the Challenger. Several specimens were then collected in three successive dredgings off the eastern coast of the United States of America on blue mud in depths of 2270 to 2470 m. These specimens all belonged to one and the same species, which was described under the name of *Porcellanaster ceruleus* by Wyville Thomson in 1877 in his preliminary account of the results of the work of the Challenger in the Atlantic. The generic name was suggested by the porcellaneous conspicuous marginal plates which have proved characteristic of all members of the group, and the specific name was suggested by the cobalt-blue colour of the specimens while alive (a colour which probably primarily has been due to the stomach content of blue mud shining through the thin body-wall, all porcellanasterids being "mud-swallowers").

Since the porcellanasterid sea-stars are limited to bathyal and abyssal levels, they have hardly ever been caught except in the deep-water dredgings of collecting expeditions, and the history of their exploration is therefore closely connected with the history of the great deep-sea expeditions. The principal expeditions having collected porcellanasterids are (with the number of dredgings in which they were taken added in parentheses):

The Challenger 1872-76 (14)
The Talisman 1883 (8)
The Ingolf 1895-96 (8)
The Investigator 1890-1903 (21)
The Princesse Alice 1895-1910 (13)
The Valdivia 1899-1900 (6)
The Albatross 1899-1911 (36)
The Swedish Deep-Sea Expedition 1948 (on the Albatross) (3)

Further also the following expeditions, research-wessels and collectors, have brought back porcellanasterids: the Travailleur 1880-81 (2), the Albatross 1883-84 (42), the Siboga 1899-1900 (3), STANLEY GARDINER about 1900 (1), the Scotia 1904 (2), the Thor 1906 (1), the Pieter Faure about 1910 (2), the Hirondelle II 1912 (1), the Arcturus 1925 (1), the Godthaab 1928 (1), the JOHN MURRAY Expedition (on the Mabahiss) 1935 (1), and the Atlantis 1947 (1).

In this paper is now added the records of the porcellanaterids collected by the Galathea 1950-52 (27 dredgings) and by the Pickle 1920 (1 dredging). Porcellanasterids are further collected in several dredgings during the recent Russian explorations of the Pacific, primarily on the Vitjaz.

In the Atlantic, porcellanasterids were collected in the area south of Greenland and Iceland by the Ingolf (73 specimens from eight dredgings in depths of about 1500 to 3200 m) and the Godthaab (4 specimens from one dredging in 2750 m in the Davis Strait). In the northwestern region off the coast of the U.S.A. a number of specimens were taken by the Challenger in three dredgings in 2270 to 2470 m, and an unknown number by the Albatross[1] in 42 hauls from depths between 1660 and 3520 m. In the eastern region of the North Atlantic, from off France to the Cape Verdes, they were collected by the Thor (2 specimens from a dredging south of Ireland in 1800 m), by the Travailleur (2 specimens from two dredgings in about 2000 m in the Bay of Biscay), by the Talisman (17 specimens from eight dredgings in about 1500 to 4800 m), by the Princesse Alice (30 specimens from thirteen dredgings in depths of about 3500 to 6035 m), by the Hirondelle II (a single specimen from west of Madeira in 5300 m), and by the Atlantis (7 specimens from a single dredging south of the Azores in 3200 m). In the tropical mid-Atlantic the Swedish Deep-Sea Expedition on the Albatross collected 40 specimens at three stations in about 4450 to 5600 m. In the eastern tropical Atlantic the Valdivia collected 33 specimens in 2275 to 4990 m in three dredgings in the Gulf of Guinea, and the Challenger a few specimens in three dredgings in 4300 to 4660 m in the Cape Verde and the Cape regions. In the Cape region 2 specimens were obtained in two dredgings in about 1500 to 1800 m by the Pieter Faure. In the Antarctic, in the Atlantic section, the Scotia collected 4 specimens in two dredgings in about 3850 and 2580 m.

In the Atlantic, the Galathea collected 71 porcellanasterids in six dredgings in the region of the Gulf of Guinea, in depths of 1260 to 5160 m, and the Pickle got some specimens in one haul in the Cape region in 2175 m.

In the Indian Ocean, the Investigator collected more than fifty porcellanasterids in the Arabian Sea and the Bay of Bengal in twenty-one dredgings from between about 1200 and 3650 m. The Murray Expedition collected 40 specimens in a single dredging in about 3850 m in the northern region off East Africa, and the Valdivia 3 specimens in three dredgings in the equatorial region off East Africa and at Sumatra, in depths of about 1650 to 5250 m. STANLEY GARDINER obtained 2 specimens from a depth of about 1000 m or more near Mauritius. The Challenger caught a single specimen in the Antarctic region in 3570 m.

In the Indian Ocean, the Galathea collected 285 specimens in fifteen dredgings distributed along East Africa, from Ceylon to the Bay of Bengal, and south of Java, in depths of 2600 to almost 7000 m.

In the Pacific, porcellanasterids were collected in the region of the Malay Archipelago by the Siboga (13 specimens in three dredgings in depths of about 1150 to 1900 m), and in the Philippine area by the Albatross in 1911 (9 specimens in five dredgings in depths of 905 to 1350 m). The Challenger collected some porcellanasterids in seven dredgings in 1460 to 5030 m, distributed from New Guinea to Japan, in the mid-Pacific, and off Chile. The Albatross collected 209 specimens in thirty-one dredgings in the eastern Pacific from the Bering Sea to off Peru and

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[1] H. L. CLARK in 1923 notes that he has examined specimens of *Porcellanaster cæruleus* belonging to the Blake collections, but possibly the Albatross collections are meant. According to E. PERRIER in 1884 p. 272, the Blake expeditions at least did not collect any porcellanasterids in the West Indian region.

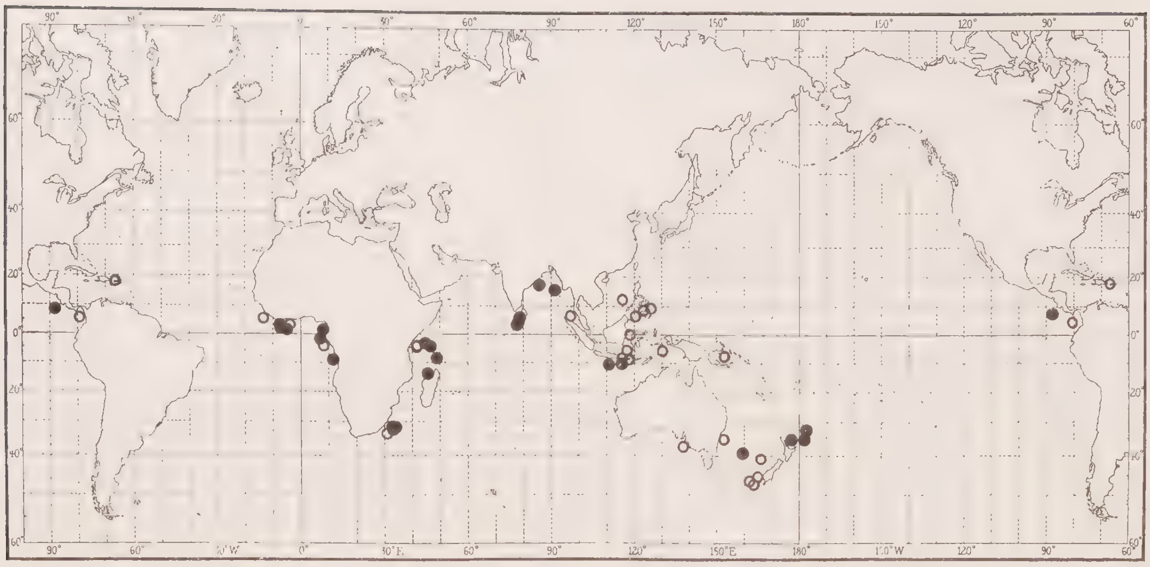

Fig. 1. Map showing the distribution of the 74 successful dredgings undertaken by the Galathea in depths of more than 1000 m. Filled circles indicate the dredgings yielding porcellanasterids.

as far west as the mid-Pacific, in depths of 1400 to 5870 m. The Arcturus got a single specimen in 3170 m in the Galapagos region. The recent Russian explorations have yielded a large material of porcellanasterids from the region of the Kamchatka and the Kuriles.[2]

In the Pacific the Galathea collected 113 specimens in five dredgings in the Australia-New Zealand region and in one dredging in the Panamic region, in depths of 2640 to about 6700 m.

Prior to the Galathea Expedition porcellanasterids were collected in about 167 dredgings, viz. 93 in the Atlantic, 27 in the Indian Ocean, and 47 in the Pacific (10 of the latter dredgings being in the region of the Malay Archipelago). The total number of specimens known at this time was probably about 600-650. The Galathea Expedition obtained porcellanasterids in 27 of the 74 successful dredgings carried through in depths of more than 1000 m, and collected a total number of 469 specimens. (Fig. 1).

The depths of the Galathea dredgings in which porcellanasterids were collected were as follows (with the total number of successful dredgings carried through added in parentheses):

1 between 1000 and 2000 m (10)
6 between 2000 and 3000 m (13)
9 between 3000 and 4000 m (15)
8 between 4000 and 5000 m (21)
1 between 5000 and 6000 m (10)
2 between 6000 and 7000 m[3] (5)

Records of depths are available for 123 of the about 167 dredgings from which porcellanasterids were reported before the Galathea Expedition.

2 were from 905 and 936 m respectively.
30 between 1000 and 2000 m
27 between 2000 and 3000 m
30 between 3000 and 4000 m
23 between 4000 and 5000 m
10 between 5000 and 6000 m
1 in 6035 m

Most of the dredgings of porcellanasterids prior to the Galathea Expedition yielded only one single valid species each. More than one species were obtained in only 28 of the recorded 167 dredgings, viz. two species in 19 dredgings (belonging to the same genus in five cases), three species in 7 dredgings (two species of the same genus in one case, otherwise all three species of different genera), and four species in 2 dredgings (two of the species of the same genus in both cases). In about half, i. e. 13 out of the 27 dredgings of porcellanasterids made by the Galathea Expedition, however, more than one species were secured (which may be considered a proof of the efficiency of the collecting-gear used by the expedition), viz. two species in 5 dredgings

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[2] Some preliminary information of this material is given e. g. by ZENKEVITCH, BIRSTEIN & BELIAEV in 1955, so that it has been possible to mark some of the finds in the accompanying maps of distribution.

[3] The specimens from the two hadal dredgings (6000-7000 m) are mentioned in the Galathea Report vol. 2, in which is dealt with the animals of the extreme depths.

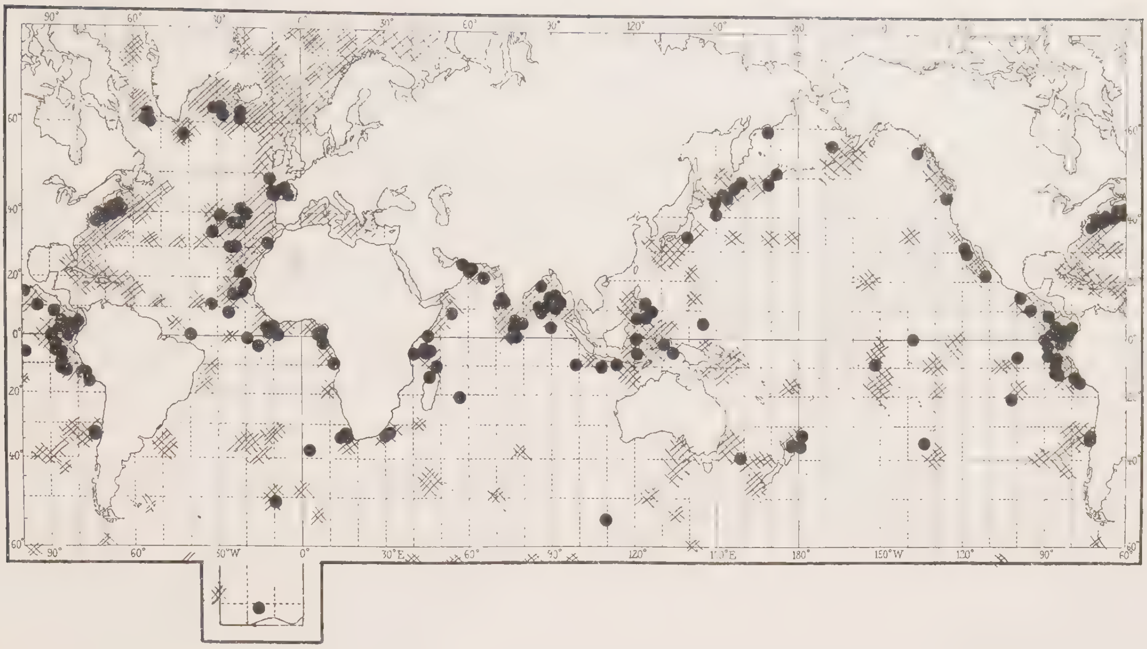

Fig. 2. Distribution of the localities from where porcellanasterids have been obtained. The cross-hatched areas indicate where deep-sea collecting has been undertaken hitherto.

(belonging to the same genus in one case), three species in 4 dredgings (two of the species of the same genus in one case), four species in 3 dredgings (two species of the same genus in one case), and five species in 1 dredging (viz. st. 282 in the Indian Ocean, at which 59 specimens of the genera *Hyphalaster, Abyssaster, Thoracaster, Styracaster,* and *Porcellanaster,* were brought up).

The present author has himself reported on the 40 specimens of porcellanasterids collected by the Swedish Deep-Sea Expedition, and has further had the opportunity to re-examine the specimens collected by the Ingolf, the Thor, the Godthaab, and the Valdivia. Through the courtesy of dr. Deichmann of the Museum of Comparative Zoology at Harvard, the author was enabled also to examine specimens of three different forms of porcellanasterids from the Albatross expeditions in the eastern Pacific. Thus the author has had a total of 628 specimens passing through his hands and has examined representatives of all porcellanasterid genera recognized, except the two bathyal genera: *Lysaster* and *Benthogenia.*

The principal authors who have dealt with the Porcellanasteridae, after Wyville Thomson had described the first one, the type of the group, are the following:

1) Sladen (1883, 1889) who took over the working up of the Challenger material of sea-stars when Wyville Thomson due to illness had to give it up, 2) E. Perrier (1884, 1885, 1894) who described the materials collected by the Travailleur and the Talisman, 3) Wood-Mason & Alcock (1891, 1893) who dealt with the collections of the Investigator, 4) Koehler (1907, 1908, 1909, 1921) who treated the specimens collected by the Princesse Alice, the Hirondelle II, and the Scotia, and also revised those of the Investigator, 5) Ludwig (1905, 1907) who reported in detail on the earlier collections of the Albatross in the eastern tropical Pacific, and preliminarily considered some of the later Albatross collections, and also the Valdivia material, 6) Fisher (1905, 1907, 1911, 1913, 1919, 1928) who treated some other Albatross collections, especially from the northern East Pacific and the Philippine region, and also dealt with the Arcturus find, and 7) Lieberkind (1932, 1935) who treated the Ingolf material and also worked up the final report on the Valdivia collection. Further reports on porcellanasterids including descriptions of new forms were published by 8) Bell (1909), (who was not aware, however, that he dealt with a porcellanasterid), 9) by Döderlein (1921), who reported on the Siboga material, and 10) by Macan (1938) who reported on the collection of the John Murray expedition. Finally, also the following authors have reported on porcellanasterids, but without naming new forms, viz. Verrill (1885, 1895) on the Albatross collections in the N. W. Atlantic, H. L. Clark (1913, 1920, 1923) on materials from the Albatross ex-

plorations in the eastern Pacific, A. H. CLARK (1948) on the specimens from the Atlantis Expedition, DJAKONOV (1950) on a specimen from the Russian explorations S. E. of Kamchatka, A. M. CLARK (1952) on the specimens originally described by BELL, and the present author (1951, 1956) on the collection of the Swedish Deep-Sea Expedition, and on the material of the Galathea Expedition from depths exceeding 6000 m. The porcellanasterids collected in the Pacific by the Vitjaz are under consideration by BELYAEV.

General remarks on taxonomy and morphology

The group Porcellanasteridae which was erected by SLADEN to embrace *Porcellanaster* and its relatives was first, in the preliminary report in 1883, registered as a sub-family of the Astropectinidae. But in 1889, in the final edition in the Challenger report in which SLADEN gives a new classification of the Asteroidea, the Porcellanasteridae are listed as the second family of the order of Phanerozonia, comprising two sub-families, the Porcellanasterinae (= Porcellanasteridae sensu Sladen 1883) and the Ctenodiscinae. SLADEN gives as reason for now associating the porcellanasterids s. str. with the genus *Ctenodiscus* that the structure of this sea-star in many ways indicates a community of descent and shows a much closer relation to the porcellanasterids s. str. than to the astropectinids. WYVILLE THOMSON in 1877 in his description of the first porcellanasterid had mentioned too that it seemed to be related to *Ctenodiscus*. However, SLADEN – besides noting the affinity between *Ctenodiscus* and the group of porcellanasterids s. str. – also points out that they at the same time differ so considerably that the separation into two distinct subfamilies appears justified. FISHER in 1911 noted that the Porcellanasteridae might be considered of the rank of a suborder, which he named the Cribellosa (coordinate with the Paxillosa, the Valvata, and the Notomyota, within the order of Phanerozonia), and subsequently, in 1916, he transferred the Ctenodiscinae to the Goniopectinidae (of the order of Paxillosa), and the concept of the Porcellanasteridae then became the one adopted in the present paper.

The generic names applied to the Porcellanasteridae s. str. are in their chronological order the following:

Porcellanaster Wyville Thomson, 1877
Caulaster Perrier, 1882
Styracaster Sladen, 1883
Hyphalaster Sladen, 1883
Thoracaster Sladen, 1883
Machairaster Perrier, 1884
Pseudaster Perrier, 1885
Eremicaster Fisher, 1905
Albatrossia Ludwig, 1905
Chunaster Ludwig, 1907
Albatrossaster Ludwig, 1907
Sidonaster Koehler, 1909
Lysaster Bell, 1909
Benthogenia Fisher, 1911

An additional genus, *Abyssaster* gen. nov., is erected in this paper for some of the species hitherto referred to *Hyphalaster,* and the description by BELYAEV of another genus, *Vitjazaster,* for a new species from the West Pacific, *V. djakonovi*, is in press.

The genera *Ctenodiscus* Müller & Troschel, 1842, and *Pectinidiscus* Ludwig, 1900, which may be found listed as porcellanasterids, belong to the group Ctenodiscinae now referred to the family Goniopectinidae of the suborder Paxillosa.

A number of the above listed generic names have fallen into synonymy, thus *Caulaster* was based on a juvenile *Porcellanaster, Machairaster* is a simple synonym of *Styracaster, Pseudaster* was based on a juvenile *Thoracaster. Albatrossia* was probably based on a juvenile *Porcellanaster, Albatrossaster* was merely a new name to replace *Albatrossia,* and *Chunaster,* as will be demonstrated in the following. is identical with *Styracaster*.

The four genera which SLADEN recognized within the Porcellanasteridae: *Porcellanaster, Styracaster, Hyphalaster,* and *Thoracaster* (with 6, 2, 4 and 1 species respectively) all stand, only his *Porcellanaster* has been subdivided into *Porcellanaster* s. str. and *Eremicaster,* and his *Hyphalaster* will in the following be separated into *Hyphalaster* s. str. and *Abyssaster*. Also nearly all the species recognized by SLADEN are valid. In fact, already the material collected by the Challenger Expedition was so representative of the porcellanasterid fauna of the deep-sea that up to this time it has not been possible to add anything of much importance to the account which SLADEN gave in his outstanding report. The Challenger material thus included representatives of all the abyssal genera of porcellanasterids described to this day[4];

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[4] The Vitjaz collections, however, include a new abyssal porcellanasterid genus: *Vitjazaster* Belyaev, in press.

the remaining recognized genera which were not represented in the Challenger collection, viz. *Sidonaster, Lysaster,* and *Benthogenia,* being – so far as is known – confined to the deeper bathyal zone.

The three porcellanasterid genera established by PERRIER all have proved to be synonyms of formerly described ones, and probably also all his nine species are only synonyms. The single genus described by KOEHLER is valid, but less than half of the ten species, he named, are so. One of the two species described by WOOD-MASON & ALCOCK is valid, while the other is uncertain. Both two genera erected by LUDWIG fall into synonymy, and only about one-third of the thirteen species, he described, can be maintained. The two genera erected by FISHER are both valid, and so are also two of the three species he described. The single species (and genus) described by BELL is distinct. But neither the single species described by DÖDERLEIN and nor the two forms described by LIEBERKIND can be maintained, and also the single species described by MACAN is uncertain.

Diagnosis:

The Porcellanasteridae (= suborder Cribellosa) are five-armed phanerozoniate sea-stars with very conspicuous, large thin porcellaneous marginal plates, and are primarily distinguished by the presence – in each arm angle – of one or more of the so-called cribriform organs.

The cribriform organ is a term created by SLADEN in 1883 for a peculiar structure present in each arm-angle of all porcellanasterids (and in this special form not found in any other group of sea-stars). WYVILLE THOMSON when in 1877 he described the first porcellanasterid, *Porcellanaster cæruleus,* noted the close covering of spinelets on the marginal plates in the arm-angles as a conspicuous character. He spoke of it as an ornament, and he also compared it to a little brush. It was SLADEN, however, who first gave a detailed description of the structure.

Every cribriform organ consists of a number, e. g. 20-30, of close-set skin folds or rows of minute papillae situated on a pair of adjacent marginals, to both sides of the vertical sutures between them, extending (in the case of fully developed organs) from the dorsal edge of the superomarginal plates to, or almost to the ventral edge of the inferomarginal ones, inwardly supported by microscopic calcareous papillae (compressed spinelets or plates), and outwardly clothed with a ciliate epithelium. Laterally each cribriform organ has a fringe of usually at least slightly larger and more robust and often flattened calcareous papillae (spines, or possibly fairly broad plates). This outer series, possibly united by a distinct web, may extend from the dorsal edge of the superomarginal plate to the ventral edge of the inferomarginal one, on either side of the organ, or – as is generally the case – it bends round close to the ventral edge and continues along the lower end of the cribriform organ up on its other side to the dorsal edge of the other superomarginal plate. The cribriform organs are thus rather indistinctly marked off from the spine- or paxil-bearing disk area, whereas they are usually well demarcated ventrally.

The cribriform organs are developed on more or less marked depressions on the marginal plates. The fringe of covering papillae can be bent away from the ciliated series of papillae or lamellae, so that these are fully exposed. But the ciliated epithelium can also be well protected by the series of papillae or lamellae being closed down upon each other in direction towards the vertical suture medially, and the covering papillae closing down upon them laterally. (Very aptly, the lamellae have been compared to the leaves of a book).

There is only a single cribriform organ in each arm-angle in *Porcellanaster* and *Sidonaster,* whereas there are three cribriform organs in each arm-angle in *Eremicaster* (though in juvenile specimens initially only a single one, and in very large (old) specimens occasionally as many as five organs). Three cribriform organs in each arm-angle similarly is the normal number in some species of *Abyssaster* and *Styracaster*. But other species of these two genera may have up to eleven cribriform organs in each interradius, and then the number often increases with age. The two only known specimens of *Lysaster* had in each arm-angle seven cribriform organs, which is one at every interbrachial vertical suture. The only known full-grown specimen of *Benthogenia* had cribriform organs developed around every single one of all the vertical marginal sutures of arms as well as of disk.

New cribriform organs are normally formed bilaterally to either side of the initial series of organs, and always around successive vertical sutures, no case being known of a suture having been skipped. In all the genera just mentioned there is a mid-interradial vertical suture, and therefore there is normally an odd number of cribriform organs in each interradius. In the genus *Thoracaster* there is a marginal plate mid-interradially, and thus an even number of cribriform organs in each interradius is the rule here, – in grown-up specimens often 12-16; but exceptionally up to e. g. 24, in which case cribriform organs occur also proximally in the arms.

The outermost and youngest cribriform organs are usually composed of a smaller number of rows of papillae than the innermost ones, and are often quite rudimentary, e. g. yet consisting of only a single row of papillae to the proximal side of the vertical sutures. The rudimentary cribriform organs are also sometimes formed from the ventral margin, in which case the rows of papillae decrease in number in vertical direction and may not yet reach the superomarginal plates. In other cases the rows of papillae are formed simultaneously from the ventral and the dorsal margins; occasionally they are formed first from the dorsal margin, and exceptionally their median part, at the horizontal suture, is the first to become developed. The width of the cribriform organs increases with age of the sea-star, so that in large (old) specimens of several forms the innermost cribriform organs often show a tendency to merge together, especially medially around the horizontal suture, but sometimes also dorsally and ventrally, and exceptionally only in these latter places.

Sladen (1883 p. 217 and 1889 p. 128) noted concerning the structure of the cribriform organ that the component parts in *Porcellanaster* (i. e. *Porcellanaster* s. str. and *Eremicaster)* were strictly lamellar in form (the calcareous compressed papillae supporting the ciliated folds placed end to end together and thus forming an apparently continuous lamella), while they were papilliform (composed of distinct, free and independent papillae) in *Hyphalaster* (i. e. *Hyphalaster* s. str. and *Abyssaster), Styracaster* and *Thoracaster*. – This holds true in broad outline, but it may sometimes be difficult to decide whether a certain cribriform organ is of a lamelliform or of a papilliform structure. In some specimens of *Styracaster* for instance (cf. p. 115) the cribriform organ must be described as lamelliform; and the supplementary cribriform organs which are sometimes formed in large specimens of *Eremicaster* (cf. p. 154) are papilliform as distinct from the lamelliform structure of the three organs which normally occur in the genus. In *Sidonaster* the cribriform organ is of a papilliform structure with very long and slender papillae, arranged very distinctly in quincunx. (The papilliform cribriform organs may also be described as spiniform).

Sladen noted (1883 p. 217, 1889 p. 128) that "The number of cribriform organs present in each angle appears to be always constant in a species; and species exist which possess 1, 3, 5, 7, 9 or even 14 of the organs respectively". Sladen himself, however, records a variation of from 7 to 9 cribriform organs in his *Styracaster horridus,* so that a concept of a specifically fixed number of cribriform organs should not be taken too literally. The larger materials of porcellanasterids which have later become available, also show that the number of cribriform organs not only increases with age, but is also subject to individual variation in equal-sized specimens, and may even vary in the different interradii of the same specimen. In general the number of cribriform organs if exceeding three in each interradius can be considered as inconstant and be expected to vary individually.

In the species in which there is a larger number of cribriform organs, three, five, or maybe even seven such organs become developed simultaneously in each interradius in the juvenile specimens, often with the series in the interradius with the madreporite formed slightly earlier than those in the other interradii.

It appears from this account of the cribriform organs that their number is only of little – if any – importance in the taxonomical description of a species, and that also a character as their width is of no specific value.

The original porcellanasterids probably had cribriform organs developed at every marginal suture (corresponding to that the related Goniopectinidae and Astropectinidae have fascioles between all the marginals). In the recent porcellanasterids a great number of cribriform organs therefore may be considered the more primitive feature, while the possession of only a single cribriform organ in each arm-angle may perhaps be regarded as a paedomorphic feature established during evolution. (The recent porcellanasterid genera with many cribriform organs also include those with the least specialized adambulacral and oral armature).

The cribriform organs appear in the living porcellanasterids as yellowish or orange vertical bands on the otherwise usually pale greyish or pale yellowish pink animal. In the preserved specimens they may be marked off by being covered with mud caught in their slime secretion.

Sladen notes (1883 p. 216) about the cribriform organ that "it is not improbable that it functioned as a percolator; and in such a case it might perhaps be looked upon as the homologue of the minute spines which border the vertical furrows that run between the consecutive marginal plates in *Astropecten* and other forms."

GISLÉN (1924) studied the feeding behaviour of *Ctenodiscus* – a very sluggish animal, with a simple type of cribriform organs, and like the deep-sea porcellanasterids a mud-swallower. When laid down on a natural mud bottom *Ctenodiscus* ploughed itself half way down into the mud. And when picked up again, it could be seen that the ciliary grooves (or the fasciolar channels) of the ventral side (which extend from the marginal sutures to the ambulacral grooves) were filled with mud glued into strings of mucus. Mud stuck together by mucus was further present around the podia, and the mouth was covered by a veil of mucus leading into the stomach. GISLÉN notes that quite probably the respiration is provided for by the ciliary currents created by the cribriform organs (in accordance with SLADEN'S view that the cribriform organs served to purify the respiration water), but he stresses that it is a fact that small particles are carried along the grooves of the cribriform organs to the ambulacral groove, to be transported thence to the mouth.

LIEBERKIND (1935 p. 34) states about the simple cribriform organs in *Ctenodiscus* that "... the lamellæ are seen to be covered with a thick columnar ciliated epithelium. In numerous places amoebocytes are found, which are about to penetrate the epithelium; this might indicate that it also plays a part as a kind of excretory organ."

CUENOT (1948 p. 211) says about the cribriform organs in the Porcellanasteridae and the homologous organs in the Ctenodiscinae that "Ils doivent probablement determiner des courants nettoyeurs, car il n'y a que peu ou point de papules chez les Porcellanastérides; il est possible aussi qu'ils remplacent les papules au point de vue de la phagocytose éliminatrice, car on a remarqué qu'ils renferment beaucoup de cellules migrantes qui traversent l'épithélium."

HYMAN (1957 p. 382) follows CUENOT in stating that the cribriform organs (of porcellanasterids and *Ctenodiscus)* presumably take the place of the papulae which she considers mostly lacking in the porcellanasterids, and follows GISLÉN in stating that the cribriform organs are "assumed in the want of other evidence to have a respiratory function, as water currents pass between their lamellae" and that "possibly, however, they also serve as detritus catchers by the mucus ciliary method as is known to be the case in *Ctenodiscus*".

Now, the porcellanasterids must live as burrowers, and in the opinion of the present author the function of the complicate cribriform organs, therefore, must be to create and maintain a circulation of water around the animal in its burrow, a channel presumably being kept open to the surface by means of the apical cone or appendage (a structure to be considered later). And, no doubt the ciliary actions, besides supplying fresh water for respiration, also serve to draw down from above surface-matter to be caught in a secretion of mucus and led to the mouth (see also p. 50).

The furrow skeleton of the porcellanasterids is – like the marginal plates and the cribriform organs – very characteristic of the group as a whole, and offers at the same time one of the best specific characteristics.

The terminology used in the present paper in the descriptions of the different skeletal elements is the same, in the main, as commonly used in modern literature on sea-stars. Only the adambulacral and oral skeletal elements are preferred termed ossicles instead of plates, these skeletal parts not at all being plate-shaped. On the other hand, all movable calcareous parts found on these ossicles and on the marginal plates etc., may be termed spines, even if they are not spiniform but e. g. granuliform or spatulate. Also the term papilla, however, may be used for such parts, as for instance in the cribriform organ. The terms 'actinal' and 'abactinal' are in the literature in general use for the oral and aboral sides, or ventral and dorsal sides, which latter designations are employed in the present paper. The term 'ray' is often used for the radial prolongations which more commonly, and also here, are called arms. Most other terms used presumably are self-explanatory.

The adambulacral ossicles are fairly large. The proximal ones are in contour rather subrhomboid in most genera, whereas the more distal ones are rather subcrescentic, with a narrower distal part and a distinct concavity aborally on their furrow side to give room for the tube-foot; and all the adambulacralia are shaped in this way in *Eremicaster, Porcellanaster,* and *Sidonaster*.

On their furrow edge the adambulacral ossicles bear a series of from two to about six so-called adambulacral spines or furrow spines. All furrow spines and oral spines are united by a more or less distinct basal web. In the genera with rather subrhomboid adambulacralia *(Hyphalaster, Benthogenia, Lysaster, Thoracaster,* and *Abyssaster)* the furrow spines are subequal in shape and uniformly spaced, so that they together form a continuous straight or wavy series along either side of the furrow. In *Styracaster* the adoral protruding margin of the adambulacralia bears two or a few close-set spines, whereas the aboral part is naked or with a single or a few isolated larger spine(s). In *Porcellanaster, Eremicaster,* and *Sidonaster,* the furrow spines are always exclusively confined to the protruding adoral part of the adambulacral ossicle, and the distal part of the furrow margin naked. In *Porcellanaster* s. str. the furrow spines may form pedicellariae; and in *Eremicaster* the distal one may be modified as a so-called segmental papilla (see below), so that here there is only a single spine to protect the tube-foot.

The furrow spines are raised at right angles to the ventral surface when the furrow (the ambulacral groove) is opened and the tube-feet (or podia) protruded, but are bent down and crisscrossed over the furrow when the tube-feet are retracted. The ambulacral groove may also be entirely shut in by the adambulacral ossicles of either side arching over it and almost meeting, possibly being a little displaced in relation to each other so that the protruding adoral part of one ossicle fits into the aboral concavity of its opposite companion. The ambulacral groove when fully expanded may occupy the whole of the ventral side of the arms, and may then, in *Styracaster* and *Porcellanaster* e. g., show a petaloid appearance.

The adambulacral ossicles on their ventral surface may bear a subambulacral armature of spinelets or granules in a varying number, but they can also all be naked without exception as e. g. in the genera *Porcellanaster, Eremicaster,* and *Sidonaster.*

The adambulacral ossicles increase in number with growth of the sea-star by new ones being formed in front of and below the terminal ossicle, and often the armature of the distal adambulacral ossicles is not yet fully developed.

The oral ossicles of the porcellanasterids are large and as a rule very conspicuous. Their shape is fairly uniform throughout the group and has been described as ax-shaped or coulter-like (the exposed surface). The two ossicles, oralia, which form the jaw usually meet proximally and medially, between which two places of contact there is an often fairly broad suture. The oral ossicles in each combined pair, however, may have their whole proximal half in an almost continuous contact, or they may join each other only at their most proximal end. The sutural part of the oral ossicle is raised more or less abruptly above the main ventral surface, and each jaw thus shows a prominent broad median keel or rounded protuberance. Each of the oral ossicles bears on its margin a series of from a few to about fifteen spines (so-called oral spines). The proximal one of these, the mouth-spine, is usually by far the largest. The other, lateral ones are generally subequal, and similar to the proximal adambulacral spines. In some genera the lateral oral spines may be modified as so-called segmental papillae (see below). In *Porcellanaster, Eremicaster,* and *Sidonaster,* the two oral ossicles forming a jaw bear only a single mouth-spine in common on their proximal junction (but two mouth-spines, one to each ossicle, may occur on some jaws, perhaps as an atavism). When the mouth is closed the marginal oral spines interlock and protect the peristome.

The oral ossicles may be provided with a varying number of spines or spinelets on their ventral surface (the suboral armature), sometimes – in large specimens of *Thoracaster* e. g. – forming a close covering. However, the surface of the oralia in *Porcellanaster, Eremicaster,* and *Sidonaster,* is always naked.

The primary oral ossicle (fig. 3*k-n*) is generally well exposed between the distally diverging oralia, and this is a special feature of the Porcellanasteridae. This skeletal element (the primary oral ossicle as it is termed by FISHER 1911 p. 27 e. g., or – as called by authors – impaired interbrachial ossicle, first interbrachial ossicle, first intermediary ossicle, or odontophore) was distinctly and correctly described by SLADEN, but in later papers it nevertheless may be seen described as a ventrolateral plate. It is best observable in dried specimens, whereas it may be obscured by the integument in specimens in alcohol. In *Hyphalaster* and *Thoracaster,* it may sometimes bear a few spinelets, but generally its surface is naked. It is of a fairly uniform appearance throughout the group, triangular with two basal lateral wings on which the oral ossicles are articulated. (Concerning the oral skeleton see further p. 49).

Segmental organs: SLADEN (1883 p. 226, 1889 p. 128) recorded from his *Porcellanaster crassus* and *P. gracilis* (now both referred to *Eremicaster)* a special modification of the surface of some of the oral and adambulacral ossicles and of their spines, which he termed the segmental pits and papillae and described as follows: "These are peculiar structures situated on the adambulacral plates and the mouth-plates. They consist of a pit which occupies the median area of the ambulacral plate, and is guarded by a small scale-like papilla articulated on the surface of the plate at the side of the pit nearest the furrow. The papilla is capable of being shut down, closing the cavity or pit like a lid; but as to the function of these organs I am quite ignorant. The

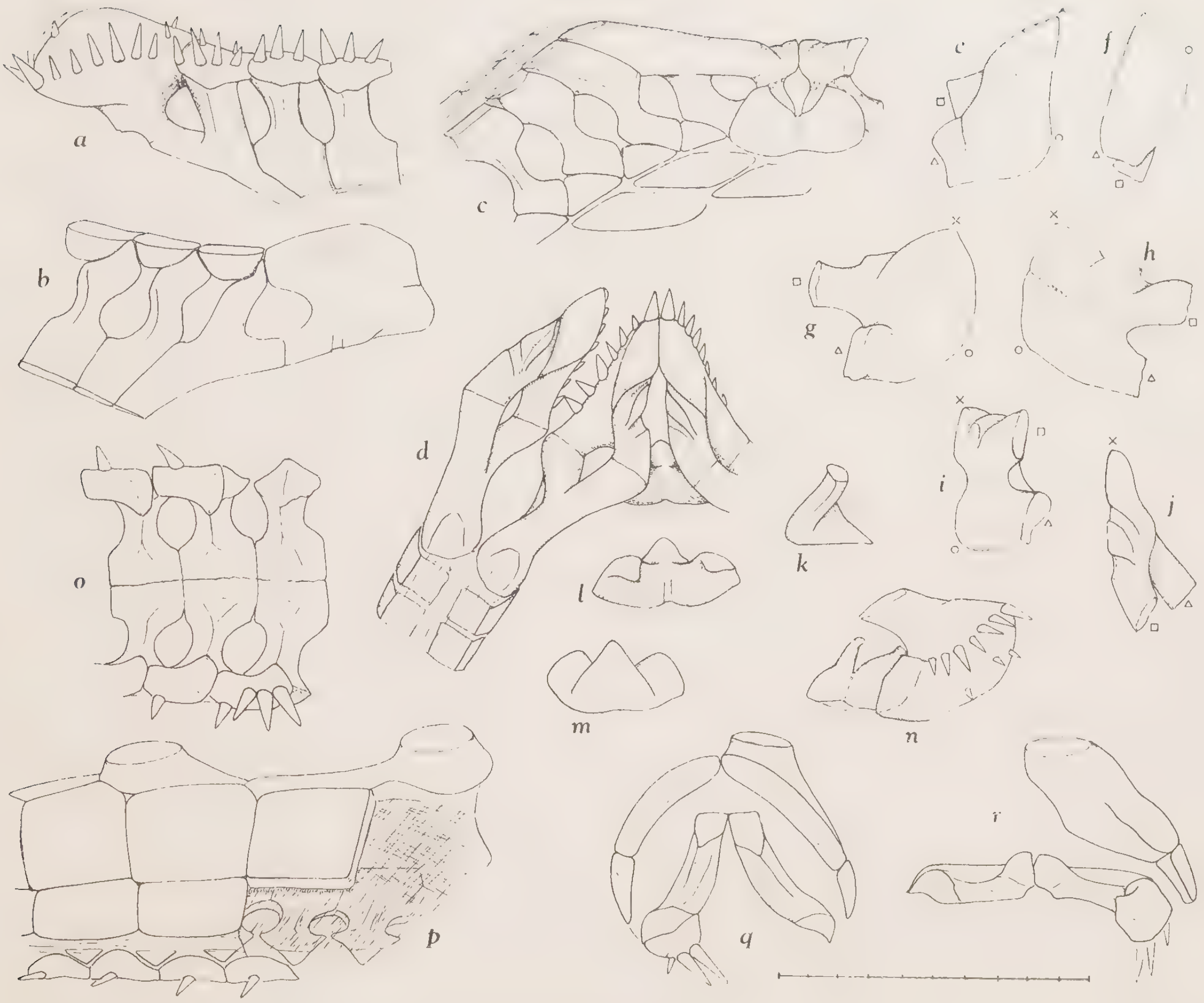


Fig. 3. Skeletal elements of medium-sized specimens of *Styracaster chuni* (R ab. 60 mm) from Galathea st. 99: a) Oral and circumoral ossicles with proximal ambulacralia and adambulacralia, as seen from the furrow side; b) same from the interradial side. c) Part of oral frame as seen from the interradial side; d) same in dorsal view. e-j) An oral ossicle in different views; e, ventral side as usually represented in the figures; f, slightly more turned; g, furrow side; h, interradial side; i, distal end; j, dorsal side; × marks the proximal end where the proximal marginal spine is placed; ○ marks the distal interradial (or the medial) part of the exposed surface, adjacent to the proximal end of the primary oral ossicle; △ marks the distal radial end, in e, f, g with the facet adjacent to the first adambulacral ossicle exposed, in i, j with the facet joining the ventral fork of the circumoral ossicle exposed; □ marks the distal dorsal end which joins the dorsal fork of the circumoral ossicle. k-l-m) A primary oral ossicle, in lateral view, in dorsal view and in ventral view respectively. n) An oral ossicle with the primary oral ossicle in position, as seen from the furrow side. o) Three pairs of ambulacralia with adjoining adambulacralia in ventral view (partly the same as shown in fig. p), furrow spines are shown on only one ossicle, while the subambulacral spine appears on all of them. p) Basal part of an arm, with the superomarginal plate no. 5 and the inferomarginals nos. 5-6 removed on the left side so that the entire ambulacral ossicles are exposed. q) An arm in cross-section, with the furrow closed, seen in aboral view, showing a pair of opposite superomarginals, one of them having borne an arm spine, the adjoining inferomarginalia, a pair of ambulacralia, and an adambulacral ossicle proximal to one of them. r) Basal part of an arm in cross-section, with the furrow opened, seen in adoral view, showing a superomarginal plate of the first joining pair, the accompanying inferomarginal plate, a pair of ambulacralia, and an adambulacral ossicle.

cavities are filled with a dark-coloured substance which may be either foreign or excreted matter."

LUDWIG (1905 p. 93), when considering the said structure, wrote that "Der Boden dieses Grübchens trägt einen feinen, weichen länglichen Wulst von unaufgeklärter Bedeutung, der offenbar von den gewölbten Plättchen beschütz wird."

The possession of these so-called segmental organs was considered a character of generic value by LUDWIG. It has been found, however, that they are of a very unstable occurrence. Within one and the same population they may be developed on adambulacral ossicles for a very varying length of the arms and may also in some specimens be totally absent (replaced by spiniform spines). In the literature the said organs are recorded only from specimens of the genus *Eremicaster*; but also the adambulacral armature in *Abyssaster tara (Hyphalaster t.)* and in *Styracaster horridus* (syn. *Chunaster scapanephorus)* may be described as forming segmental organs.

Fisher (1911 p. 25) in his description of the adambulacral plates of his *Eremicaster tenebrarius (= E. gracilis)* states that there is "one segmental papilla which is transformed into a spinelet distally on ray"; but, naturally, the reverse is the case, viz. that it is the aboral and normally spiniform furrow spine which on the more proximal adambulacral ossicles is modified as the spatulate spine called a segmental papilla.

The segmental papillae in *Eremicaster* obviously are homologous to the aboral spiniform furrow spines, and actually the so-called segmental organs may have no special function at all, the segmental papilla merely being a structural variant of the spine (cf. p. 50). In those specimens of *Porcellanaster* s. str. in which the furrow spines form pedicellariae, these too may be laid back into a pit on the surface of the adambulacral ossicles, corresponding to the segmental pit in *Eremicaster* into which the segmental papilla fits.

The ambulacral ossicles (fig. 3 *o, q, r)* are rather dumb-bell-shaped. Their radial lateral end is cut squarely so that the opposite joining ones become in direct continuation of each other when the furrow is fully opened; all the ambulacralia then together forming a flat floor in the bottom of the furrow. Their median narrow part leaves room for the single series of pointed podia to each side in the furrow. Their interradial lateral end is cut obliquely adorally and aborally and join up to the aboral and adoral ends of two successive adambulacralia respectively. The lateral ends of the ambulacral ossicles may then appear as small triangular "plates" outwards of, and alternating with the adambulacralia. Sladen does not mention anywhere in his text that the ambulacralia in the porcellanasterids thus may be visible between the adambulacralia, but the feature appears from his pl. 20A figs. 9 and 10, showing the ambulacral and the adambulacral ossicles of a specimen of *Porcellanaster cæruleus* in different views, and fig. 2 showing a specimen of the same species in ventral view; further also from pl. 24 fig. 2 showing a *Styracaster armatus* in ventral view.

Since Sladen did not explicitly point out the visible ends of the ambulacral ossicles, some later authors have fallen into the trap of considering them a series of ventrolateral plates (e. g. Perrier in 1894 with regard to *Styracaster,* and Döderlin in 1921 with regard to *Porcellanaster* and *Sidonaster)* or as supplementary adambulacral plates. The misinterpreted ends of the ambulacral ossicles – when observed in some specimens – have been considered of specific taxonomic importance too, as e. g. when Lieberkind in 1935 on the basis of this character supported Perrier's species *Porcellanaster granulosus.* The only reference and correct description of the visible ends of the ambulacral ossicles (common in more or less marked degree to all porcellanasterids) was given by Fisher (1911 pp. 26 and 30) with regard to his *Eremicaster tenebrarius* and *E. pacificus.*

Superambulacral ossicles do not seem to be present in any of the genera of the Porcellanasteridae s. str. (i. e. with *Ctenodiscus* and allies removed).

The marginal plates of the porcellanasterids are large and thin, subquadrate, subrectangular or subrhomboid. Usually they form an even contour to the body, and the sutures are often indistinct until the specimens are dried. The superomarginal plates and the inferomarginal ones are as a rule of about equal size in the arm angles, whereas in the arms the inferomarginals become progressively lower than their superomarginal companions, the plates of both series diminishing gradually as they proceed along the arms. In well expanded specimens the marginal skeleton forms a gently rounded or perpendicular wall to the body, the dorsal and ventral surfaces of which slope upwards and downwards from it respectively. In specimens with empty stomach the height of the marginal skeleton may represent the height of the body, and the marginal plates may even arch somewhat over the dorsal as well as the ventral side.

The superomarginal plates of either side of the arm, from about the fifth or sixth opposite pair, meet in several genera in the median dorsal interradial line, and are then more or less curved (fig. 3*q)* and the first ones which encase the arm higher, to a varying degree, than those bordering the disk. The joining of the opposite superomarginals, which gives the arms the characteristic narrow shape, is a peculiarity of *Hyphalaster, Lysaster, Benthogenia, Thoracaster,* and *Styracaster,* and is a feature met with in only few other sea-stars.

The superomarginals may be armed with one or a few erect spines or spinelets, placed on or near their dorsal edge. The possession of a superomarginal spine-armature is to some degree a character of age, and is also often individually variable in full-grown specimens of the same population. The character is therefore not always of much taxonomic value. In *Styracaster* the arm spines are erect, immovably fixed, and arranged in a single row along the mid-dorsal arm-line; the spine-bearing plates being larger than the opposite ones and reaching over the midline. The number of arm-spines usually vary somewhat in different specimens from the same population, but there is in this genus (i. e. in all specimens known) at least one dorsal spine on each arm, belonging almost without exception to the first pair of joining superomarginals. The marginal plates are otherwise except for the dorsal spines and the cribriform organs in general naked, only in *Thoracaster* there may be a more or less developed armature of spinelets on the superomarginal as well as on the inferomarginal plates.

The inferomarginal plates are in the arm angle situated exactly below their superomarginal companions, and the same may be the case in the arms, but here the plates of either series may also alternate more or less regularly, and the arrangement may vary in the different arms of the same specimen, even in different parts of the same arm. Similarly the superomarginal plates of either side of the arms may be placed exactly opposite each other or may subalternate, also their arrangement being individually variable. The arrangement of the marginal plates thus cannot be used taxonomically.

The first inferomarginal plates seem to be formed a little later than the superomarginal ones, and in juvenile specimens therefore also the interbrachial inferomarginals may be lower than the superomarginals. Young specimens may also show a larger number of superomarginals than of inferomarginals, whereas the reverse is the general rule in the grown-up specimens, which often have at least one or two superomarginals more than inferomarginals, in consequence of that the terminal ossicle – in front of which the new marginal plates are formed – lies more or less dorsal to the arm end.

While the normal growth of the arms takes place by the interpolation of skeletal elements in front of and below the terminal ossicle, matters may be somewhat different in the case of regeneration of lost arms. It may also in such cases happen that marginal plates form a termination of the broken arm immitating a terminal ossicle.

The shape of the arms in section is subcylindroid in most of the forms in which the arms are encased by the superomarginals, but in *Styracaster* the arms are compressed, and when here a continuous series of arm spines is developed, the arms assume a distinctly keeled shape. The arms when encased by the superomarginals, are usually sharply marked off from the disk, more or less rigid and incapable of being curved to any marked degree; only if long they may be able to curve somewhat horizontally (cf. pl. X 1-2). The arms in the other forms, in which a strip of dorsal integument extend to the terminal ossicle, are less distincly marked off from the disk, flattened or subcylindroid respectively, depending on the state of contraction or inflation of the specimen, and capable of being well curved back. Specimens of this type with empty stomachs and very much contracted, may have the dorsal integument sunk below the upper edges of the superomarginal plates and these arching over the arms so as to actually touch their opposites.

The normal feature of a marginal suture in the interradial mid-line in all genera known, except *Thoracaster* (and *Vitjazaster* Belyaev in press), apparently is subject to individual variation in rare cases, cf. figs. 6*a* and 19*a*.

The terminal ossicle is usually large, larger than in most other sea-stars, with the exception of e. g. some goniasterids. It is one of the earliest formed skeletal elements, and in the juvenile specimens it is thus relatively larger than in the adults. It changes somewhat in appearance with growth in the juveniles before assuming the final form; e. g. it has initially a concave proximal margin, also in the species in which it in the full-grown specimens is convex proximally, and it may at first be distal to the arm end, even if dorsal in position in the adults. The shape of the fully formed terminal ossicle can also vary somewhat within the species, and e. g. the number of spines borne on it may be very variable. In the different genera, however, the main appearance of the terminal ossicle is sometimes so divergent that it may be used taxonomically, though with caution, and in a few cases it may even be used in characterizing a species.

Sea-stars, when mowing about, generally keep the arm tips curved aborally in order to expose the terminal sensory podia. In the porcellanasterids the arms are rather rigid in most genera, but their distal end is then to some degree permanently aborally bent. The terminal ossicle, as noted, may be entirely dorsal to the arm end (the series of marginal plates); and if placed in a distal position, it is usually turned upwards at a more or less sharp angle, its dorsal surface sloping upwards from the main dorsal line of the arm, its ventral surface being rounded, and the ambulacral groove extending upwards on its distal end. An optical cushion was not present in the porcellanasterids examined by MEURER in 1907 *(Thoracaster magnus* (= *T. cylindratus), Porcellanaster waltharii* (= *Eremicaster gracilis),* and *Porcellanaster vicinus* (= *Eremicaster v.)).*

The ventral skeleton in the interradial area consists as a rule of a pavement of squamiform plates, and similar plates may also extend ventrolaterally in the arms in a narrow band between the adambulacralia and inferomarginalia. These two latter series of skeletal elements in the arms, however, may also be separated only by a strip of naked integument, or they may be in immediate contact. The arrangement of the component plates in the ventrolateral (ventral interradial) areas may be rather irregular. Generally, however, the plates lie in fairly distinct tangential series, parallel to the margin where new plates are formed, and further they may form fairly regular "radial" columns parallel to the interradial line, extending from the marginalia to the adambulacral and oral ossicles, in *Hyphalaster* e. g., with two radial columns of ventrolateral plates, and in *Eremicaster* e. g., with about four such radial columns corresponding with a marginal plate.

The ventrolateral plates are often hardly visible even in dried specimens, being concealed by a thick and leathery skin. They may bear an armature of spinelets, and this is a general rule in some genera, as e. g. *Thoracaster.* In some species of other genera such an armature, however, can only be considered an individual variation.

An anal opening is absent in all porcellanasterids, and also an intestine is always lacking. The center of the disk, however, is often raised into a conical eminence or a long tubular appendage, which is frequently designated as an epiproctal appendage. A tail-like appendage – appearing as a subcylindroid tube – is thus typical of *Porcellanaster* and *Eremicaster;* but the possession of a distinct apical appendage or apical cone is otherwise primarily a juvenile feature, and it may be subject to highly individual diversity. The central dorsal area, also if a prominence is lacking, is generally distinguished by an armature of very small paxillae or spiniferous plates.

The presence of an apical appendage was first mentioned in the literature by E. PERRIER in 1882 with regard to his *Caulaster pedunculatus* (= *Porcellanaster cœruleus* juv.*).* He called it the "pédoncule dorsal", and compared it to the stalk of the crinoids. SLADEN in 1883 p. 214, in his diagnosis of the porcellanasterids, mentioned it as: "A central epiproctal prominence, more or less defined, frequently developed into an elongate tubular prolongation."

WYVILLE THOMSON in his original description of *Porcellanaster cœruleus* (1877 p. 380) stated that: "the excretory opening is very prominent in the centre of the dorsal perisom of the disk," but, as SLADEN notes (1889 p. 130), this "inadvertent remark probably arose from the examination of a specimen in which the extremity of the epiproctal funnel was either invaginated or actually broken off." SLADEN also comments on PERRIER's above cited hypothesis regarding the "pédoncule dorsal," stating that it can have no morphological basis whatsoever, as the structure seems to him "to be nothing more or less than an extraordinarily developed anal funnel (whether aborted in function or not is immaterial for the present argument), and as such it is the homologue of the anal funnel of a Crinoid ...". Eventually PERRIER, in 1894 p. 201, compared and homologized the "pédoncule dorsal" to the ventral umbilical cord by which the juveniles of *Asterias spiralis* are attached to their mother animal, considering this – like the stalk of the crinoids – a modification of the praeoral lobe of the embryo.

SLADEN (1889 p. 129) says that: "Under favourable conditions, I have detected an extremely minute pore at the extremity of the tubular epiproctal prolongation in *Porcellanaster.* It is, however, so very small that I do not think it can act (in the adult at any rate) as an anal aperture, although it may probably be an excretory orifice," and p. 130 he notes "I have also found a similar pore at the extremity of the epiproctal peak in *Ctenodiscus,* and likewise in *Hyphalaster.*" FISHER (1919 p. 42), in the description of three juvenile *Benthogenia cribellosa,* notes concerning the prominent apical appendage here that "there is certainly a tiny pore at the summit," but adds "whether this is confined to immature life can not be determined." The present author similarly thinks to have observed a pore in the apical cone of specimens of *Eremicaster vicinus,* (cf. p. 164). LUDWIG (1905 p. 98), however, states with regard to his *Porcellanaster waltharii* (= *Eremicaster crassus)* that he has convinced himself through dissection and serial sections, that the apical appendage is closed at the end. He found it encasing an extension of the coelome and divided by a longitudinal mesenterial septum into two half tubes which at their bases were in wide open connection with the coelome. GOTO (1914 p. 96) when considering the apical appendage of *Ctenodiscus* notes that "In the centre of the conical abactinal prolongation one can easily distinguish in many specimens a small "pore" evidently connecting with the body cavity. This is also present in many *Eremicaster tenebrarius,* and is what SLADEN (GOTO, however, must here mean WYVILLE THOMSON) took to be an anus in *Porcellanaster.* I (GOTO) think it must be an artificial opening caused by a stretching of the abactinal membrane at the summit of the cone, and possibly subsequent wearing, as the rudimentary paxillae are usually more or less worn down here."

Since the porcellanasterids, besides lacking an anal opening, also lack any intestine, it is of course not strictly correct to speak of the tail-like dorsal appendage as an epiproctal appendage, and LUDWIG (1905 p. 90) therefore proposed naming it "Scheitelfortsatz" or "Apicalfortsatz" (in English version "apical appendage"), this being a more correct term as not hinting at any special function of the structure. HYMAN in her handbook (1957 p. 250) mentions that the structure is "of unknown significance". This is quite true, but some very probable guesses as to its function can be made, and, in fact, have been made. In the integument of the apical appendage or the apical cone is usually found a very crowded assemblage of minute calcareous deposits, similar in type but smaller than those of the main part of the disk, and this crowding of the skeletal elements in the preserved specimens is no doubt a consequence of that the organ has been strongly contracted. L. CUENOT in 1891 p. 385 mentioned the apical cone of the porcellanasterids immediately after having discussed the apical cone which can be raised temporarily in *Astropecten* as a possible tactile organ, since if it is touched this sea-star buries itself deeper down into the sand. Possibly CUENOT thus considers the apical cone of the porcellanasterids having the same function. MACBRIDE (1933 p. 402) also expressed the notion that the permanent cone of the porcellanasterids was a further development of the temporary elevation of the back of the astropectinids; not aware of the fact that already CUENOT had pointed out the homology. (Also the present author – before coming across the cited references – arrived at the obvious conclusion that the apical cone of the porcellanasterids was the homologue of the temporary cone in the astropectinids).

The apical appendage or cone is evidently capable of being much extended in the living animal; and, no doubt, a similar cone as in *Astropecten* may be raised also in those porcellanasterids in which no trace of a such is to be observed in the preserved specimens. Perhaps the apical cone or appendage in the porcellanasterids can be supposed to have a function also in keeping a channel open to the surface from their burrows (cf. p. 41). That the apical cone or appendage is relatively larger in the juveniles than in the adults, may be explained by such a function.

The dorsal armature of the porcellanasterids is somewhat varying in the different forms. In the juvenile specimens there is at first a pavement of rather large rounded perforated plates; but subsequently these become absorbed and replaced by the final skeleton, which may consist of plates, or of pseudopaxillae, or of paxillae.

The specimens described by PERRIER in 1882 under the name of *Caulaster pedunculatus,* and referred to above, were juveniles with an embryonic pavement of plates, which PERRIER homologized with the calyx of the crinoids, considering, as noted, the apical appendage homologous with the crinoid stem. PERRIER also noted that the possession of these plates was an embryonic character, and that they disappeared with age. SLADEN (1883 p. 217, 1889 pp. 130-131) rejects, however, the theory of the embryonic plates being homologous with the crinoid calyx and mentions as one of the things speaking against it that in *Porcellanaster* (and *Caulaster)* there is a dorsocentral plate, and it is with this plate alone "that any relationship with the stem of a Crinoid could exist in the apical system of an Asterid." PERRIER also compared the plates around the apical appendage of his *Caulaster* with those forming the periproct of an echinoid, but P. H. CARPENTER (1884) found that this comparison could not be maintained, as according to PERRIER's description the apical system of *Caulaster* consists, not of genitals and oculars (basals and radials) as in an echinoid, but of underbasals and basals, and SLADEN in 1889 notes that he entirely concurs with this view. However, with regard to the arrangement of the embryonic plates in the porcellanasterids, the present author agrees with LIEBERKIND, who, in 1935 p. 7, about the dorsal skeleton of juvenile *Porcellanaster cœruleus* stated that: "Whether these first rudiments of plates should be called basalia or radialia is a matter of judgment, they have no phylogenetic importance at all, and are only to be considered a natural arrangement of rudimentary plates in a radially built animal."

The permanent dorsal skeleton which replaces the embryonic one, when this is absorbed, may also partly consist of rounded perforated plates, so e. g. in the arms of *Eremicaster*. In the disk area there may be minute spiniferous plates, at first few but in older specimens more numerous, e. g. in *Porcellanaster, Eremicaster,* and *Sidonaster,* and in some species of *Styracaster*. The dorsal skin in these forms appears thin and membraneous, especially if the animal is extended by a full stomach. In well expanded specimens, e. g. of *Eremicaster,* it can be observed that the dorsal integument is crisscrossed by bands of fibrous tissue, in the interspaces between which are found the plates and the papulae. In some well-preserved specimens e. g. of *Porcellanaster*, the skin which clothes the dorsal spinelets may be seen extending far off their distal point.

The dorsal armature of the adult specimens is composed of distinctly developed paxillae in the genera *Hyphalaster, Benthogenia, Lysaster, Thoracaster, Abyssaster,* and in some species of *Styracaster*. The paxillae usually are closely crowded, but may be somewhat spaced when the animal is well expanded. In expanded specimens the spinelets of the paxillar crown, which are movably attached to the shafts, may be seen bent horizontally outwards to meet their neighbours and thus protect the surface of the animal.

As to the microscopic structure of the skeletal elements reference is made to the descriptions and figures given by LIEBERKIND in 1932 and 1935. The larger calcareous components are generally robustly built, whereas the smaller components usually are of a very open structure, the embryonic plates, as mentioned above, being perforated and the spinelets usually composed of fine rods united by short transverse dissipiments.

The madreporic body is usually conspicuous, subcircular, and with deep furrows radiating from a point located near the adcentral margin, or stretching across in radial direction. It lies close to the marginal plates, touching these or being separated from them by a few rows of paxillae, its position being individually variable.

Papulae were recorded by SLADEN from the dorsal side of his *Porcellanaster caulifer* and his *P. gracilis (= Eremicaster g.)*. Generally, however, the papulae are very difficult to observe, only showing themselves when the disk is well expanded. And when in many porcellanasterids not mentioned, it does not necessarily mean that they are really absent in these. CUENOT is not right when stating, in 1948 p. 209, that papulae are wanting in the porcellanasterids. HYMAN (1955 p. 382) notes that "In the Porcellanasteridae, which mostly lack papulae, their place is presumably taken by the cribriform organs, assumed in the want of other evidence to have a respiratory function ..." ("The papulae constitute the usual respiratory provision of the asteroids but cannot be of supreme importance as they are few in number in many Phanerozonia and wanting in some cases").

The papulae are confined to the dorsal side of the disk proper, but are always absent from the central area and the radial lines in which the stomach is attached. They emerge singly in the interstices between the paxillae or plates and are usually not very numerous. In those porcellanasterids in which the paxillae are crowded and staggered, the papulae may be present, in the areas in which they occur, in a slightly larger number than that of paxillae; in a specimen of *Hyphalaster inermis* thus each paxilla in the papular area was surrounded by 5-6 papulae, and each papula enclosed by 3 paxillae. In the forms with spaced and non-staggered plates, the papulae are at most present in the same number as that of the plates, thus a specimen of *Eremicaster crassus* shows an equal distribution of spiniferous plates and papulae in the interradial papular areas.

Papulae were observed in specimens of all the genera represented in the present material, and so their occurrence is recorded now in all the genera of the Porcellanasteridae except *Lysaster* of which, however, only two specimens are known.

Pedicellariae are recorded from a single genus only, viz. *Porcellanaster* s. str. *(Caulaster, Albatrossia)*, but they are not of a stable occurrence, some specimens possess them, others do not. They are known only from juvenile specimens and thus perhaps become lost with age. They are straight, sessile (simply two movable spines) and placed on the dorsal side, mostly interradially. Also the ambulacral spines in this genus *(Porcellanaster)* may in pairs form pedicellariae, one to each ossicle, and occasionally the oral spines may do the same.

The gonads are present in a number of ten, i. e. with a single one to each side of the interbrachial septa. (In some cases the gonad papillae were observable dorsally at the arm angles). Each gonad has the appearance of a small tuft of e. g. 6-10 unbranched or slightly branched tubules, usually 8-10 mm long at most; in e. g. a *Thoracaster cylindratus* with R 103 mm up to 12 mm long. The gonads were examined in several specimens; and supposedly ripe eggs were found in specimens of *Hyphalaster inermis, Thoracaster cylindratus, Abyssaster tara,* and *Eremicaster crassus,* all from st. 238, in *Styracaster horridus* from st. 664, in *Eremicaster crassus* from st. 217, and in *Eremicaster gracilis* from st. 716. The eggs are roundish or slightly oval, and measure up to 0.5-0.6 mm. (Ripe eggs in porcellanasterids were recorded also by Ludwig in 1905 from a specimen of his *Porcellanaster waltharii (= Eremicaster gracilis)*. Presumably, the porcellanasterids have a direct development, to judge from the egg-sizes when compared with those of other marine invertebrates of which the type of development is known (cf. Thorson 1952 pp. 282-283). Even when ripe, the gonads are not very voluminous, and the number of eggs contained in them is only small.

The tube-feet ampullae are single. (They were examined by Ludwig (1905 pp. 91, 103) in *Hyphalaster moseri (= H. inermis)* and in *Porcellanaster pacificus (= Eremicaster p.))*. Fisher included this feature as one of the distinguishing characters in his diagnosis of the Porcellanasteridae. But it has since proved (Fisher 1919) that also the Goniopectinidae have single tube-feet ampullae. (The Astropectinidae and the Luidiidae have the tube-feet ampullae double). That the tube-feet ampullae in the porcellanasterids are single has been ascertained by the present author in specimens of all the examined genera.

The polian vesicles are present in a number of two in the interradius with the madreporite (with one to each side of the stone canal which is fused to the ventral body wall) and singly in the other interradii. (Ludwig in 1905 recorded this arrangement of the polian vesicles from his *Porcellanaster pacificus* and *P. waltharii,* but stated that he did not find any polian vesicles in his *Hyphalaster moseri.* In the present study, however, polian vesicles were observed arranged as recorded whenever examined, also in specimens of *Hyphalaster inermis)*. The stone canal is rather calcified and may be visible through the ventral integument, in *Porcellanaster* and *Eremicaster* e. g.

The stomach, which fills out the entire disk, consists in the porcellanasterids of a single undivided cavity which has the dorsal wall closely attached to the dorsal body wall. There is not the least trace of intestinal caeca. Fisher (1928) noted about *Thoracaster* that "There is no dorsal chamber of the stomach similar to that which is characteristic of most sea stars. Instead the dorsal wall is closely juxtaposed to the wall of the disk as in the Ophiuroidea"; and this description seems to fit every porcellanasterid. From the stomach extend in each arm the usual pair of pyloric caeca (hepatic c., radial c., or brachial c.), cf. fig. 10, pl. 4 in Lieberkind 1935, which shows a specimen of *Styracaster chuni* in which the dorsal body wall has been removed.

Parasites: The parasitic chaetopod *Myzostoma* has been found in the present material on specimens of *Hyphalaster inermis* from sts. 52 and 282 in the Atlantic and the Indian Ocean respectively, and on specimens of *Abyssaster tara* from st. 238 in the Indian Ocean. (Koehler in 1908 mentions tumors on his *Hyphalaster scotiae* as probably caused by an infection with *Myzostoma)*. An Athecate Hydroid was commensalistic on some specimens of *Eremicaster gracilis* from the Panamic region (cf. p. 160). Dendrogate Ascothoracids, the internal crustacean parasites, were found in some dissected specimens of *Hyphalaster inermis* from sts. 30 and 52 in the Atlantic and from st. 282 in the Indian Ocean respectively; and in a specimen of *Eremicaster crassus* from st. 238 in the Indian Ocean. Also an *Eremicaster gracilis* from st. 716 in the Panamic region appears to be infected with these organisms. (Fisher in 1919 p. 35 recorded *Dendrogaster* from *Sidonaster vaneyi)*.

Remarks on the supposed mode of life: The porcellanasterids – being phanerozoniate sea-stars – have an adambulacral peristome, which means that the most prominent skeletal parts of the frame surrounding the oral aperture centrally on the ventral side (mouth, actinostome) is formed by the five interradial jaws or pairs of oral ossicles, which again are connected by the radially situated circumoralia or "first vertebrae", composed of the fused first and second ambulacral ossicles, (fig. 3*c, d)*. The skeletal frame around the mouth can be either constricted or widened to a rather considerable degree (the structure being articulated on the five primary oral ossicles). The oral membrane, or peristome, which is expanded between this frame is very dilatable, and, as seen from some specimens, can be distended into a wide funnel leading into the stomach. In case of full stomachs it may lie as a thin web over the stomach content. When Fisher in 1928 discussed the skeletal frame around the mouth of *Thoracaster,* he stated that the ambulacral elements here were longer than he had noted in any other sea-star and that the whole frame was unusually flexible. He therefore concluded that fairly large objects could be ingested.

All porcellanasterids are mud-swallowers. Curiously enough, Sladen in his report on the Challenger material did not make any references whatsoever to the fact that the stomach of these sea-stars is often found completely filled with mud. But it has repeatedly been noted by later authors. Fisher, op. cit., recorded in a *Thoracaster* (of which, however, no size was given) a stomach content of 9 ccm mud (with various organic matter as foraminiferans, diatoms and radiolarians). In the examined Galathea material e. g. an amount of 14 ccm mud was found in a specimen of *Styracaster horridus* with R/r 91/21 mm. The mud in the stomachs always contains many foraminiferans, calcareous and sandincrusted forms, and also radiolarians; in addition sometimes minute snails, and bits of worm tubes, and also sponge spicules and different parts of sea-urchin skeletons e. g. The latter elements, however, may have been taken as dead debris, and this of course may apply also to the other items mentioned. One small *Porcellanaster cæruleus,* R/r 11/4.5 mm, however, in its stomach had the remains of a comparatively large sea-urchin which it must have swallowed whole. The porcellanasterids thus may also act as scavengers and perhaps be facultative predators. Plant debris was found in some stomachs, e. g. a 23 mm long and 1 mm thick twig in a *Hyphalaster* with R about 65 mm.

Many sea-stars feed wandering about on the surface and by adhesion to the podia selecting and picking up organic matter, which then by coordinate movements of the podia is passed to the mouth; and e. g. the sand-dwelling *Astropecten* (a distant relative of the porcellanasterids), though it spends most of its time buried in the bottom, always ascends in order to feed.

The mud-swallowing porcellanasterids, on the contrary, most certainly do not leave their burrows for feeding. And since they can hardly be considered just swallowing the bottom material below them (which would be of small value as food), there is every reason to believe that they are able to secure from above the surface material comparatively rich in organic matter. The water circulation produced by the ciliate cribriform organs (cf. p. 41) therefore no doubt also serves in maintaining a constant flow of matter from the surface down to the sea-star so that it may be caught in the mucus secretion and subsequently led to the mouth by the podia. The distinct spineless lines which ventrally in the most spiniferous specimens of *Hyphalaster* extend from the cribriform organs to the furrow correspond to the ciliary grooves in *Ctenodiscus,* cf. p. 41.

In some stomachs much of the content was found in the form of minute balls of detritus-like substance, but though these might be considered swallowed food pellets formed by the podia, they rather are faecal pellets derived from the ingested bottom material, the deep-sea floor presumably being covered with faecal pellets in quantities. When the organic content in the swallowed material has been utilized the whole stomach content must be ejected through the mouth, and before feeding again the animal probably moves forward sufficiently to obtain the surface material from another place.

The porcellanasterids perhaps ascend regularly in order to change position and make a new burrow in another feeding place, or maybe they ascend only in order to spawn. The manner in which the porcellanasterids bury may reasonably be considered about the same as that of *Astropecten,* which is able to descend vertically (and rapidly), throwing the sand aside by outwards flings of the podia. In the porcellanasterids, however, perhaps also the furrow spines play a part in digging (which would explain their usually flattened shape, and perhaps their transformation into the so-called segmental organs in some genera). The porcellanasterids can no doubt also move about below the surface of the substratum. (At least, another of their distant relatives, *Luidia,* is able to glide, even surprisingly quickly, through the sand under its surface).

Some examined porcellanasterids with supposedly ripe or almost ripe gonads had their stomachs completely filled with bottom material, and so the periods of sexual activity probably have no influence on the feeding activity. The gonads even when supposedly ripe are also only small in relation to the animal. A greenish substance, the secretion from the pyloric caeca, may be found in otherwise empty stomachs.

The long-armed porcellanasterids often have the arms at different stages of regeneration, and so they are evidently easily broken in life, perhaps during burrowing, perhaps due to attacks by enemies.

The colour of the porcellanasterids usually is pale greyish or pale yellowish pink, or possibly reddish orange (or faint purplish), and with a darker (in *Porcellanaster* and *Eremicaster* dull bluish) cast on the disk when a possible stomach content shows through the thin skin; and with the cribriform organs light orange or yellowish.

On the taxonomic value of various characters, the ratio R/r, etc.: In the description of a sea-star the size is usually given as R/r = x/y mm, R being the distance from the center of the disk to the arm tips (i. e. the length of the entire arms, or rays, or radius of the specimen as a whole), and r the distance from the center of the disk to the interbrachial angle (the radius of the disk). It has also been customary to record the ratio R/r in the specific diagnosis, but this should be regarded with some caution since this ratio shows a definite increase with growth, in accordance with the positive allometric growth of the arms. The figures of R/r form a very useful means, however, for characterizing the different individuals from the same catch.

Owing to distortion of the specimens, it may sometimes be difficult to record R/r with only reasonable exactness. Furthermore, the measurements are influenced by the extent to which the stomach is filled, i. e. whether the mouth frame is widely opened or closely constricted, especially the measurements of r is influenced hereby, and in the present study the measurements therefore – in specimens with a widened mouth – were taken, not from the center of the disk, but from the proximal end of the mouth-spines. The length of R usually is slightly varying in the different arms of the same specimen; and in the long-armed forms, in the cases where some of the arms have been broken off and later regenerated, the arms may be of very different lengths, and it is then the length of the longest arm which is stated. The measurements given for R in the following text should therefore not be taken too strictly, some variation should be allowed for.

The accompanying diagrams (figs. 4-5) illustrate the change in the ratio R/r (the increase in relative arm length) with growth in some species of porcellanasterids of which a sufficient number of measurements are available (from records in the literature as well as from the Galathea material). In the diagrams the figures of R/r are indicated with R measured along the horizontal axis and r along with the vertical axis. Further, the diagrams illustrate the gradual increase in the number of superomarginal plates.

It will be seen that the rate of growth as expressed by the gradual change in the measurements of R/r, is the same in *Hyphalaster inermis*, *Thoracaster cylindratus*, *Abyssaster tara*, and *Porcellanaster cæruleus*. On an average the ratio R/r in these porcellanasterids is <2 in the juvenile specimens, about 2 by R 10-20 mm, about 2.5 by R 35 mm, about 3 by R 60 mm, and increasing to about 3.5 by R 70-100 mm. Approximately, the growth as expressed by the changes in R/r follows a straight line, in the just mentioned examples with a gradient of about $^1/_4$.

The increase in number of superomarginals with growth is about the same in *Hyphalaster inermis* and in *Thoracaster cylindratus*, though in the latter slightly on the high side of the variation found in the former. These two porcellanasterids also both have slender arms encased by the superomarginals. In *Abyssaster tara* and in *Porcellanaster cæruleus* the number of superomarginals is lower than in the former forms (in equal-sized specimens) and the increase in number slower, corresponding to the fact that the arms in *Abyssaster* and *Porcellanaster* are broader, not encased by the superomarginals, which also are relatively larger.

In *Styracaster horridus*, *Eremicaster crassus*, and *Eremicaster gracilis*, there is a faster increase in the ratio R/r with growth than in the above mentioned forms, R/r being about 2.5 by R 15 mm, about 3 by R 35 mm, about 4 by R 60 mm (and in *Styracaster horridus* increasing to about 5 by R ab. 125 mm), the growth gradient being about $^1/_6$. In these forms the disk is thus relatively smaller in relation to the arm length than was the case in *Hyphalaster inermis* and the other first discussed forms.

The number of superomarginals in relation to the arm length in *Styracaster horridus*, which has slender arms encased by the superomarginals, is the same as in *Thoracaster cylindratus*. In *Eremicaster gracilis* the number of superomarginals agrees with that found in *Styracaster horridus* and in *Thoracaster*, though in *Eremicaster* the arms are not encased by the superomarginals. In *Eremicaster crassus* the number of superomarginals is slightly lower on an average than in equal-sized *E. gracilis*, agreeing with the number found in *Hyphalaster inermis*.

In the other porcellanasterids the growth-rates as expressed by the ratio R/r and the number of superomarginals are as follows: *Hyphalaster hyalinus* and *H. scotiae* agree with *H. inermis*. *Abyssaster diadematus* and *A. planus* agree in the ratio R/r with *Abyssaster tara*, but apparently have a slightly larger number of superomarginals in relation to the arm length. *Styracaster caroli* and *S. elongatus* agree with *S. horridus*, whereas *Styracaster chuni*, *S. paucispinus*, *S. robustus*, *S. armatus*, and *S. spinosus*, all agree with *Hyphalaster inermis*. *Styracaster monacanthus* has the number of superomarginals corresponding to that which is found in *S. chuni*, but has a relatively larger disk and shorter arms, R/r being 2 by R 24 mm. *Benthogenia* and *Lysaster* too

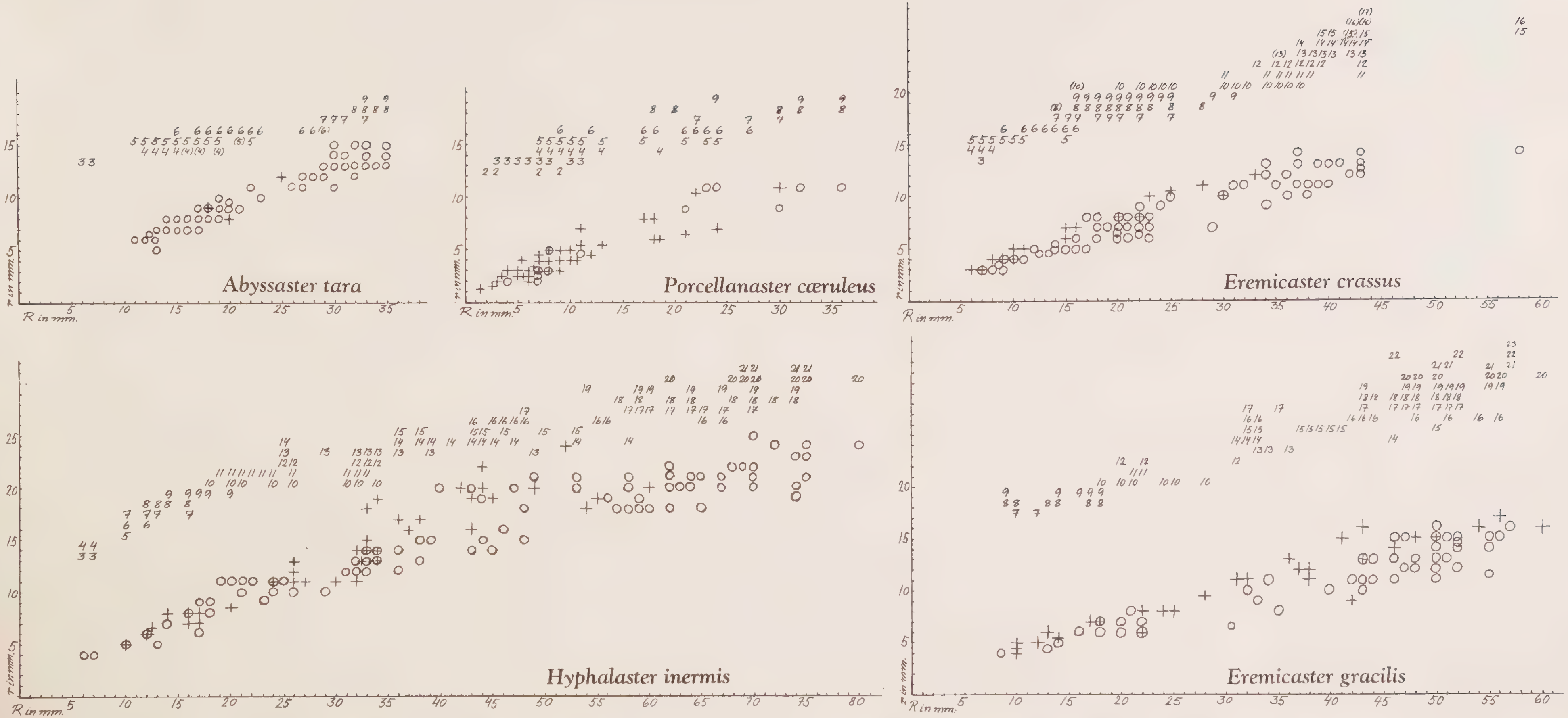


Fig. 4. Diagrams illustrating the rate of growth as expressed by the change in R/r and in number of superomarginals in *Abyssaster tara*, *Porcellanaster cæruleus*, *Hyphalaster inermis*, *Eremicaster crassus*, and *E. gracilis*. The horizontal axis gives the length of R, the vertical axis the length of r. Crosses refer to specimens recorded in the literature, circles to specimens in the Galathea material.

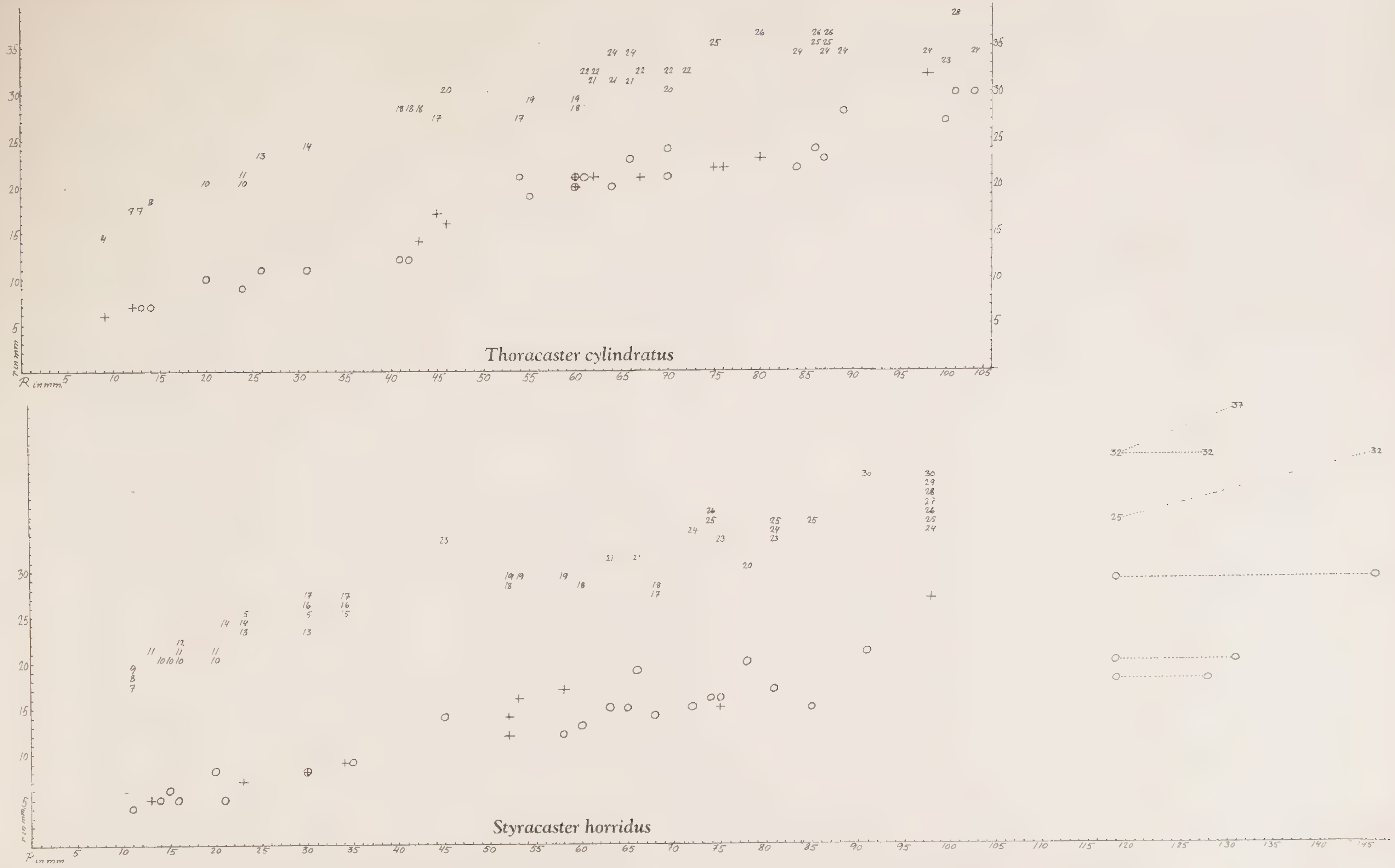


Fig. 5. Diagrams illustrating the rate of growth in *Thoracaster cylindratus* and *Styracaster horridus*. (See further the legend to fig. 4).

have a low ratio of R/r, about 2.6 in *Benthogenia* by R 78 mm (17 superomarginals) and about 2.3 in *Lysaster* by R 55 mm (11 superomarginals). *Eremicaster vicinus* and *E. pacificus* agree with *E. crassus,* and *Sidonaster* agrees with *Porcellanaster.*

The interbrachial arch (arm-angle or interradial part of the disk) may be curved inwards – in the forms with a large disk and narrow arms – if the stomach is empty, and outwards if the stomach is full. If the stomach is empty the ventral side usually slopes slightly downwards from the margin to the jaws with an inward-bending curve, but if the stomach is full the whole ventral side may be distinctly outwards curved. Similarly, the dorsal side (disk) may be flat, even depressed, if the stomach is empty; and the paxillae (if such occur) are then densely crowded; but if the stomach is full, the whole disk may be much inflated, and the paxillae are then spaced on the expanded integument. The shape of the body thus is of little or no value as a specific character.

Much information given in the descriptions or diagnoses of porcellanasterids in the literature is in fact of no specific significance, and is hardly of any individual significance either, since the descriptions concern specimens in a particular (preserved) state of contraction or expansion. Width of mouth opening, width of furrows, direction of furrow spines, position of marginals, perpendicular or arching over the disk, etc., are all characteristics which naturally change continuously in the course of the life rhythm of the animals. A number of other features used taxonomically previously, change with growth, e. g. the appearance of the dorsal skeleton, number and also form of the marginal plates besides their spine-armature, to some extent also the number of cribriform organs. All such characters should therefore be considered with caution.

During the present investigation it appeared that still other characters, previously considered of taxonomic value, may actually be so variable within the species that they can only with the greatest reservation be used for a specific discrimination; for instance the presence of absence of segmental organs, the number of dorsal arm spines, the state of the ventral armature, and in some cases the presence or absence of a ventrolateral skeleton in the arms.

The porcellanasterids in the available material are often in a rather poor condition, which is not surprising as these animals from the deep-sea may have spent hours in the trawl in the warm upper waters of the tropical sea before reaching the deck. The long-armed forms are seldom caught intact, some arms are nearly always lost, or found broken off in the content of the dredge; and since this is the general rule, it has not been found of any interest to call special attention to it in the descriptions, but it will clearly appear from the accompanying photographs.

Remarks on the genera recognized, their distribution and interrelationship: Up to this date 15 genera and 57 species of porcellanasterids have been named in the literature. The following revision resulted, however, in a division of the group into only 9 genera and less than 25 valid species. The Galathea collection consists, as noted above, of 469 specimens; and these fall into 11 species and 6 genera. None of the species are new to science.

Of the recognized genera, *Benthogenia, Lysaster,* and *Sidonaster*, belong to the bathyal zone, and appear in their regional distribution restricted to the region of the Indian Ocean inclusive of the Malay Archipelago.

All the other genera occur in the abyssal zone, and all of them (except the still undescribed *Vitjazaster)* are known to be widely distributed in the deep-sea. They are *Hyphalaster, Thoracaster, Styracaster, Abyssaster, Porcellanaster,* and *Eremicaster.*

The present author, as mentioned above, has been able to examine a fair number of the known forms of Porcellanasteridae, having had representatives of all genera except *Benthogenia* and *Lysaster* at his disposal. Furthermore, in the Galathea collections some populations have been represented by adequate series of individuals so that it has been possible to form a fair idea of the infraspecific variation.

Many sea-stars are known to be rather polymorphic, with short- and long-armed specimens, spiny and paucispine ones, or some with pedicellariae and others without, occurring side by side. Polymorphism also proved a pronounced feature in some of the forms of porcellanasterids now examined, and actually it is a quite remarkable infraspecific variation which has been found in some of the larger samples of single populations.

The cosmopolitan nature of several of the abyssal species of porcellanasterids was demonstrated through the direct comparisons of widely separated populations, which the Galathea material made possible.

The Porcellanasteridae constitute a rather homogeneous group, and all the forms are undoubtedly of a monophyletic origin. Two main groups may be distinguished. The first group comprises *Benthogenia, Lysaster, Hyphalaster,* and also *Thoracaster,* which all show a similar general appearance and are distinguished only by such characters which do not seem to be very important in principle. These genera no doubt are the most primitive of the recent porcellanasterids, and *Benthogenia* then probably the most primitive of them all. *Styracaster* may be referred to this same group, though it is more specialized; and also *Abyssaster* should be ranged here, though showing some special features. The second group comprises *Porcellanaster* s. str., *Eremicaster,* and *Sidonaster,* which all resemble each other very much in general appearance. They have only a small number of cribriform organs, and may show a specialized furrow armature. Hence they may be considered phylogenetically younger than the former group, though perhaps not younger than *Styracaster* (and *Abyssaster).*

The presumably older abyssal genera, *Thoracaster* and *Hyphalaster,* comprise only a single and a few species respectively, and these show rather constant characters (i. e. the monotypic *Thoracaster,* and *H. inermis* which is the only species of *Hyphalaster* known in more specimens) while a younger genus as *Styracaster* comprises a larger number of species, and another young genus, *Porcellanaster,* constitutes an apparently monotypic, but polymorphic group.

On the presentation of the material: In the following descriptions of the Galathea material it has been attempted always to adhere to the same sequence of presentation, viz. size, marginal skeleton, cribriform organs, terminal ossicles, dorsal skeleton, a possible dorsal prominence and papulae, adambulacral, oral, and ventral skeleton, possible biological remarks and distribution. The same order has been followed in the summaries of the descriptions in the literature, in which also the often different terminology has been transcribed into that used in the present paper. It should in this way be fairly easy to find the reference to any character wanted, and to compare the different descriptions. The descriptions given of the genera supplement the diagnoses, but do not repeat information given there.

In the descriptions of the various samples it has been tried to avoid unnecessary repetitions of what may be common to all species of a genus. In spite of this, some descriptions at first sight may appear more lengthy than perhaps worth while. It has been found necessary, however, to treat several characters, especially the spine-armature, in detail so that the variation in individuals and in populations might be demonstrated, and in that way proof given of the various specific identifications, and also to avoid the doubt which might arise as to some characters, if no reference was made to them.

Attention has been paid to various abnormalities, since these might throw light on some specific interrelationships, and also because some nominal species have been based alone on e. g. irregularities in the arrangement of the marginal skeleton. Several of the present specimens showing individual variations might undoubtedly easily (and erroneously) have been described as representing new species, if they had been dealt with separately and not as members of populations represented by more individuals, e. g. the one-spined *Styracaster horridus,* (cf. p. 98), the *Hyphalaster inermis* with mirror-shaped furrow spines (cf. p. 69), or the *Eremicaster gracilis* with a ventrolateral spine-armature (cf. p. 158).

Key to the recognized genera of Porcellanasteridae

(The key considers the fully developed specimens only)

Page

1a. Superomarginals of either side of arm joining in the radial midline from about the fifth or sixth opposite pairs. Furrow narrow. Cribriform organs rather papilliform. A mouth-spine to each oral ossicle 2
  2a. Superomarginals unarmed, or with small dorsal spines, forming a double row in the arms. Arms subcylindroid. Adambulacralia subrhomboid-subcrescentic, and with a continuous row of subequal furrow spines. Paxillae, or possibly pseudopaxillae on disk 3
    3a. Mid-interradially a set of odd marginal plates. No larger superomarginal spines. Cribriform organs confined to the interbrachial marginals . . . . *Thoracaster* 82
    3b. Mid-interradially a marginal suture 4
    4a. Superomarginals of arms unarmed, those of disk possibly with a small spine. Cribriform organs confined to the interbrachial marginals . . . . *Hyphalaster* 56

Page

4b. Superomarginals of disk unarmed; but at least some of those of arms with a dorsal spine 5

5a. Cribriform organs confined to the interbrachial marginals .... *Lysaster* 80

5b. Cribriform organs developed on all marginals clear to the terminal ossicle. *Benthogenia* 81

2b. Superomarginals with one or several, robust erect spines placed in the midline of the arms, from the first pair of joining plates and outwards. Arms possibly compressed. Adambulacralia of arms with a protruding adoral part with close-set furrow spines, and an aboral part with a single or a few isolated spines. Paxillae, pseudopaxillae or spiniferous plates on disk. *Styracaster* 92

1b. Superomarginals of either side of arm separate to terminal ossicle 6

6a. Two mouth-spines, i. e. one to each oral ossicle. Superomarginals unarmed. Furrow spines in a continuous series. Paxillae on disk. 3-7 papilliform cribriform organs .. *Abyssaster* 72

6b. A single mouth-spine to the combined pair of oralia forming a jaw. Superomarginals possibly with a dorsal spine. Adambulacralia with a protruding adoral part to which the furrow spines are confined. No suboral or subambulacral armature. Spiniferous plates or pseudopaxillae on disk 7

7b. A single large cribriform organ of a papilliform structure. Terminal ossicle subcrescentic .... *Sidonaster* 165

7a. One or three cribriform organs of a lamelliform structure. Terminal ossicle rather tubercular 8

8a. Three cribriform organs .... *Eremicaster* 143

8b. One cribriform organ .... *Porcellanaster* 123

The genus *Vitjazaster* Belyaev (in press), which in this key would be placed besides *Abyssaster*, has a set of odd marginal plates mid-interradially, where all other porcellanasterids, except *Thoracaster*, have a suture. It is further distinguished from all other porcellanasterids hitherto described by having paxillae also ventrally.

SYSTEMATIC PART

Hyphalaster Sladen, 1883, emended

Type-species: *Hyphalaster hyalinus* Sladen, 1883.

Diagnosis:

Porcellanasterids with superomarginals forming a complete casing to arms, unarmed, but those of disk possibly with a dorsal spinelet. A mid-interradial suture. Cribriform organs (5-11) confined to disk marginals.

Description:

The specimens of this group have a subpentagonal disk with the arms well set off, subcylindroid, of a rather uniform thickness throughout, and with the terminal ossicle placed rather distally, forming a blunt end, armed with 3, occasionally 5 spines. The cribriform organs are papilliform. The inferomarginals of the arms are only slightly lower than their superomarginal companions. The body is flat when the stomach is empty, the perpendicularly placed interbrachial marginal plates deciding its height, but even when the stomach is full the shape of the body usually do not become pronouncedly tumid. The genus is known to attain a size of R about 90 mm. The proportion of R to r ranges from hardly 2 in juvenile specimens to somewhat more than 3 in large ones. The dorsal side is armed with close-set, well-developed paxillae, or with pseudopaxillae or spiniferous plates. Juvenile specimens show an apical appendage, medium-sized specimens generally show a more or less distinct apical cone, while larger specimens are often devoid of any central prominence. The jaws show a well prominent broad rounded keel formed by the interradial and greater part of the two oral ossicles, which meet proximally and medially, being separated by a wide suture between the two places of contact. Distally the triangular surface of the primary oral ossicle is well exposed. There are 5-12 marginal oral spines, the proximal one the largest, the others subequal to the furrow spines. The adambulacralia have a subrhomboid to subcrescentic contour, and bear 3-6 furrow spines. All the furrow spines are connected by a well-developed basal web, and form a continuous wavy series along the narrow furrow, which may be almost completely closed in by the overarching adambulacralia. The ventrolateral area is rather wide and paved with imbricating transversely elongate plates, arranged in tangential and in radial rows, which latter correspond two and two with the adjoining marginal plates. A narrow strip of small ventrolateral plates may also extend a varying distance down the arms. The ventrolateral plates are typically spiniferous, and also the surface of the oralia and the adambulacralia bear spinelets in the grown-up specimens. There is a fairly thick integument ventrally, and the contours of the jaws, adambulacralia, and ventral plates therefore are often more or less indiscernible.

Remarks:

SLADEN in 1883 erected the genus *Hyphalaster* to embrace his four species: *hyalinus, diadematus, inermis* and *planus,* and later the following other species (or nominal species) have been ascribed to the same genus, viz. *parfaiti* and *antonii* by PERRIER in 1885, *tara* by WOOD-MASON & ALCOCK in 1891, *valdiviae* by LUDWIG in 1900 (in CHUN), *moseri* by LUDWIG in 1905, *fortis, gracilis,* and *scotiae* by KOEHLER in 1907 (*a* and *b*), and *giganteus* by MACAN in 1938.

The form from the Valdivia Expedition which CHUN in 1900, p. 490, listed as *Hyphalaster valdiviae* n. sp. (on basis of LUDWIG's preliminary identification of it) was in reality a specimen of SLADEN's *Thoracaster cylindratus* (according to LUDWIG in 1907); and also the *Hyphalaster* n. sp., which RICHARD in 1903, p. 66, mentions from a Princesse Alice dredging, was a *Thoracaster cylindratus,* as it appears from the final report on the Princesse Alice material by KOEHLER in 1909*b*.

The other forms (not all specifically valid, as will be discussed in the following) fall into two groups as to the appearance of the arms. In one group the superomarginal plates join their opposites along the dorsal midline of the arms from about the fifth or sixth plates, whereas in the other group they all remain separate to the terminal ossicle. These two groups must be considered generically different. The former group, for which SLADEN's generic name *Hyphalaster* must be retained, comprises SLADEN's species *H. hyalinus* (the type-species), and his *H. inermis,* and further all later described species except *H. tara.* The latter group, for which the name *Abyssaster* is created, comprises besides WOOD-MASON & ALCOCK's *H. tara,* which is designated as the type-species of the genus, also SLADEN's *H. diadematus* and *H. planus.*

The group *Hyphalaster* s. str. is recorded from dredgings in all three oceans; and several individuals have often been obtained in a single catch. SLADEN's two species, *hyalinus* and *inermis,* were both from the Pacific and appear well distinct. PERRIER's *parfaiti* was from the Atlantic, but, as will be demonstrated in the following, it is evidently the same species as *inermis.* LIEBERKIND (1932 and 1935, in two of the more recent papers on porcellanasterids) discussed the Atlantic records of *Hyphalaster* in detail, and arrived at the conclusion that they all belonged to one and the same species, which he listed as *H. parfaiti,* and of which then *antonii, fortis* and *gracilis* are considered synonyms. The remaining species of *Hyphalaster* s. str., not discussed by LIEBERKIND, are besides the type-species *hyalinus: H. inermis, H. moseri, H. scotiae,* and *H. giganteus. H. inermis* includes, as noted, in the present authors opinion, *parfaiti,* further also *moseri,* and perhaps also *giganteus.* Thus only three valid species of *Hyphalaster* s. str. may be known at present, viz. *H. hyalinus, H. inermis,* and *H. scotiae.*

The Galathea Expedition obtained specimens of *Hyphalaster* s. str. in altogether 15 of the 27 dredgings yielding porcellanasterids (five in the Atlantic, eight in the Indian Ocean, and two in the south-western Pacific). All these specimens appear to belong to one and the same species, which is recorded here under the name of *H. inermis.*

Key to the species of *Hyphalaster* s. str. — Page

1 a. Disk with spiniferous plates and pseudopaxillae. Interbrachial superomarginals with spines. *hyalinus* 58
1 b. Disk with paxillae. Interbrachial superomarginals unarmed.................................. 2
2 a. Subambulacral spines almost as large as the furrow spines, two to each ossicle, and forming a continuous series parallel to the furrow.................................. *scotiae* 72
2 b. Subambulacral spinelets markedly smaller than the furrow spines, more than two to each ossicle, and usually rather irregularly arranged.................................. 3
3 a. Ventrolateral plates spiniferous.................................. *inermis* 58
3 b. Ventrolateral plates unarmed.................................. *giganteus* 72

Hyphalaster hyalinus Sladen, 1883

Sladen 1883 pp. 235-237, 1889 pp. 156-159, pls. 26_{1-6}, 28_{13-16}.

This species was described from two specimens dredged at the Challenger st. 274 in the tropical mid-Pacific (7°25′S, 152°15′W, 5030 m, radiolarian ooze, 1.7° C.).

The type-specimen has R/r 20/10 mm; 8 superomarginal plates, joining their opposites from no. 6, and the two innermost to each side of the interradial suture with a dorsal, horizontally directed spinelet; proximal marginalia twice as long as high, distal ones higher than long; 7 narrow cribriform organs. Fairly large tumid terminal ossicle with 3 spines. Disk with spiniferous small plates (spicules) and pseudopaxillae with up to 4 spinelets; no apical cone. Adambulacralia subcrescentic, with 3 furrow spines (4-5 are shown in fig. 2 pl. 26) and 3-5 spinelets on their surface (18 adambulacralia according to the figure). Oralia with 6 marginal spines, and suborally about 3 spines along the suture and some few granules distally. Ventrolateral area with a plating of imbricating subhexagonal scales, each with 2-3 or a few more granules. A narrow strip of ventrolateral plates extending to the terminal ossicle.

The other specimen has R/r 12/15 mm, and, judging from fig. 4-5 pl. 26, 8 unarmed superomarginalia, 11-12 adambulacralia, all with naked surface, and also bare ventrolateral scales. A complete embryonic dorsal plating of scales. No apical appendage.

The type-specimen apparently is rather expanded due to a full stomach, and this partly accounts for Sladen's description of the dorsal membrane as thin and almost transparent, and of the pseudo-paxillae as being well spaced. Sladen (1889 p. 159) notes that he is not quite sure of the specific identity of the juvenile specimen, but probably there is no reason why this should be doubted.

H. hyalinus is distinguished by the dorsal spinelets on the interradial superomarginal plates, and by the dorsal armature of spiniferous plates and pseudopaxillae. Also the shape of the proximal superomarginalia, twice as long as high, may distinguish *H. hyalinus* from *H. inermis,* in which the proximal superomarginalia are generally subquadrate. In *H. hyalinus* the ventrolateral plates extend to the terminal plate, whereas in similar-sized specimens of *H. inermis* they usually extend only a short distance outside the disk area.

Hyphalaster inermis Sladen, 1883

Figs. 6-7. Pls. I-III, XIII 3-4

H. inermis n. sp., Sladen 1883 pp. 239-242; 1889 pp. 162-164, pls. 25_{4-6}, 28_{5-8}.

H. parfaiti n. sp., E. Perrier 1885 *a* p. 886 (nom. nud.); 1885 *b* pp. 65-67; 1894 pp. 229-232, pl. $16_{2\,a\text{-}e}$.

H. antonii n. sp., E. Perrier 1885 *a* p. 886 (nom. nud.); 1885 *b* pp. 61-64; 1894 pp. 232-235, pl. $16_{1\,a\text{-}e}$.

H. sp., Albert 1902 p. 963 = *H. antonii* + *H. fortis,* Koehler 1907.

H. moseri n. sp., Ludwig 1905 pp. 100-103, pl. 7_{36-37}.

H. fortis n. sp., Koehler 1907 pp. 14-16; 1909 *b* pp. 30-31, pl. 16_{1-2}.

H. gracilis n. sp., Koehler 1907 pp. 16-18; 1909 *b* pp. 32-33, pl. 14_{5-6}.

H. antonii, Koehler 1909 *b* pp. 29-30.

H. fortis, Koehler 1921 p. 2.

H. gracilis, Koehler 1921 p. 2.

H. parfaiti, Lieberkind 1932 pp. 282-285, textfig. 9, pls. 1_{5-6}, 3_{4-11}, 6_{1-4}.

H. parfaiti, Lieberkind 1935 pp. 19-26, textfigs. 6-8, pls. 1_{7-9}, 3_{1-11}, $5_{9,\,11-14}$.

H. parfaiti, A. H. Clark 1948 pp. 75-76.

H. parfaiti, Madsen 1951 p. 82.

? *H. giganteus* n. sp., Macan 1938 pp. 331-333, pl. $1_{3,\,7}$.

non: *H. parfaiti,* Albert 1902 p. 962, and Richard 1902 p. 86, = *Albatrossaster richardi* Koehler, 1909 (a juvenile *Porcellanaster cæruleus*).

Sladen's description of *H. inermis* was based on two specimens from the Challenger st. 237 off Japan (34°37′N, 140°32′E, 3430 m, blue mud, 1.8° C.). The type-specimen has R/r 20/8.5 mm; 9 superomarginalia, joining from the 5th opposite pair, proximal ones subquadrate; 7 cribriform organs. Fairly large, somewhat tubercular terminal ossicle with 3 short spines. Dorsal side with closely crowded small paxillae with 5-10 spinelets. (See also p. 71). An apical cone. Adambulacralia with 3-4 furrow spines, and the proximal subrhomboid ones with a single subambulacral granule adorally. Oralia with 7-8 marginal spines (fig. 6 pl. 28 only shows 6), and 1-2 suboral granules. Ventrolateral plates subhexagonal and with 4-5 granules. No ventrolateral plates in arms. The other specimen has R/r 10/5 mm, and 5 superomarginalia. Several specimens were taken in the haul, according to the summary of the scientific results of the expedition.

H.moseri: The only other Pacific record of *Hyphalaster* s.str. hitherto (besides those of *H.hyalinus* and *H.inermis* just mentioned) is that of two specimens from the Albatross st. 3684 in the mid-Pacific (0°50′N, 137°54′W, 4504 m, globigerina ooze) on which Ludwig (1905) based his species: *H.moseri.* They have R/r 26/12 and 32.5/13 mm respectively; 10 and 11 superomarginalia, joining their opposites from nos. 5-6; 9 cribriform organs. Terminal ossicle with 3 spines. Dorsal side with close-set paxillae with 6-8 spinelets. An apical cone. Adambulacralia with 4 furrow spines (in arms 3) and 3-4 subambulacral spinelets. Oralia with 7 marginal spines, and suborally 2-3 spines along sutural and some minute spinelets along distal margin. Ventrolateral plates with 4-6 spinelets.

Ludwig noted that this new species was nearest to Sladen's *inermis,* but distinguished by a richer ventrolateral and oral armature. When, however, the larger size of Ludwig's specimens is considered, this difference (apparently the only one) is of no importance. It therefore seems reasonable to regard *H.moseri* as a synonym of *H.inermis.*

H.giganteus: In the Indian Ocean only a single specimen of *Hyphalaster* s.str. has hitherto been recorded, viz. by Macan (1938) who described it as representing a new species, *H.giganteus,* though at the same time noting its close affinity to the Atlantic *H.parfaiti.* It may be merely an individual variation of this form (= *H.inermis*), and will be discussed in more detail on a following page.

H.parfaiti: This species was described by Perrier (1885, 1894) from a single specimen dredged by the Talisman in the Bay of Biscay (st. 135 – by a lapse Perrier in 1885 writes st. 138–: 46°09′N, 9°16′W, 4787 m, grey-yellow mud). The unique type has R/r 55/19 mm; 16 superomarginalia, joining their opposites from nos. 5 (-6), slightly longer than high; 9 cribriform organs. Terminal ossicle fairly small and with 3 short spines. Dorsal side uniformly covered with small paxillae with 7-9 granules. A faint apical cone. Adambulacralia subrectangular, with 4 flattened subequal furrow spines, and usually an irregular row of 5-6 slender subambulacral spinelets along the interradial margin. Oralia with 7-8 marginal spines, and with 3 fairly large spines along the suture, and about 10 smaller ones over the rest of the surface. Ventrolateral plates transversely elongate and generally with 5-7 spinelets, sometimes in two parallel rows.

It appears that this specimen is distinguished from the type of *H.inermis* merely by a richer spine-armature, a difference which is accounted for by its larger size.

H.antonii: E.Perrier (1885, 1894) described this form from a single specimen from a Talisman dredging near the Azores (st. 131: 38°38′N, 27°26′W, 2995 m, soft white mud). It has R/r 16/7 mm; 9 superomarginalia, joining their opposites from no. 5; 7 cribriform organs, the two outermost ones rudimentary. Terminal ossicle with 3 short spines. Dorsal side with numerous small paxillae with 4-5 granules. A small apical appendage. Adambulacralia rather rectangular, with 4 furrow spines, and 1-3 subambulacral spinelets. Oralia with 8 marginal spines, and 3-4 granules on their surface. Ventrolateral plates subhexagonal and with 4-5 spinelets.

Ludwig (1907 p. 313 foot-note) states that he considers Perrier's *H.antonii* a juvenile *H.parfaiti.*

Under the name of *H.antonii,* Koehler (1909 *b* p.29) records two specimens of *Hyphalaster,* R/r 14/8 and 16/8 mm, from two Princesse Alice dredgings at the Cape Verdes and off the Canary Islands respectively (st. 1150: 16°12′N, 24°44′W, 3890 m, sand and mud, and st. 1789: about 31°06′N, 24°00′W, 5413 m, globigerina ooze?). Koehler is inclined to think, however, that Ludwig is right in supposing *H.antonii* to be a juvenile *H.parfaiti,* but considers it impossible to say definitely so without knowledge of intermediary stages. The specimen from st. 1150 belongs to the lot which Prince Albert in 1902 mentions as *Hyphalaster* sp.

Lieberkind (1935), after having re-examined the type-specimen, confirmed that *H.antonii* was identical with *H.parfaiti.* But something has gone wrong when he writes, p. 20, that "The number of adambulacral spinelets, of marginal plates as well as of madreporic plates, is on the other hand exactly the same in the two forms. Therefore, there is no doubt that Ludwig is right in supposing that *Hyphalaster Antoni* only is to be considered an immature stage of *Hyphaloster parfaiti.*" – The juvenile stage, of course, shows a smaller number of superomarginals than the adult, and both stages only a single madreporite, as have all porcellanasterids, so, what Lieberkind wanted to point out perhaps was that the appearances of these structures were the same in both forms.

H.fortis: This species was described by Koehler (1907, 1909 *b*) from two specimens from the Princesse Alice st. 1150 at the Cape Verdes (16°12′N, 24°44′W, 3890 m, sand and mud) – by Prince Albert in 1902 p. 963 listed as *Hyphalaster* sp. –, and further Koehler recorded some arm-fragments from the Princesse Alice st. 753 near the Azores (about 30°50′N, 18°W, 4360 m, globigerina ooze). The two specimens have R/r 60/20 and 54/18 mm respectively; 19 superomarginalia, joining their opposites from nos. 5-6, (proximal ones described as about twice as high as long, see further p. 62, those of the arms as subquadrate); 9 cribriform organs. Terminal ossicles with 3-5 spines. Dorsal side with a uniform covering of close-set paxillae with a circle of granules surrounding about 10 central ones. The smaller specimen with an apical cone. Adambulacralia subrectangular, with 4 furrow spines and 3-4 subambulacral spinelets along interradial margin. Oralia with 10 marginal spines, and 3 small conical spines along the suture. Ventrolateral plates in tangential series, polygonal and with scattered granules.

Koehler (1921) records two additional specimens of *H.fortis* from the Princesse Alice st. 2986 in the Bay of Biscay (45°07′N, 7°06′W, 4870 m).

Lieberkind (1935 p. 19), after a re-examination of some arm-fragments of the original specimens, concluded that *H.fortis* was merely a synonym of *H.parfaiti*.

H.gracilis: Koehler (1907, 1909*b*) described this species from three specimens dredged by the Princesse Alice west of the Canary Islands (st. 1787: 31°07′N, 24°03′W, 5413 m, globigerina ooze). They have R/r 32/14, 33/15 and 36/17 mm respectively; 12 superomarginalia (-14 according to Lieberkind 1935), joining their opposites from no. 5, (proximal ones described as much higher than long, see further p. 62, those of arms as only slightly higher than long); 9 cribriform organs. Terminal ossicle conspicuous, with 3 spines. Dorsal side with close-set small paxillae. The medium-sized specimen with an apical appendage, the others without. Adambulacral ossicles subrectangular, with 4 furrow spines. (According to Lieberkind (1935), who had re-examined one of the original specimens, there may also be a few subambulacral spinelets, whereas Koehler stated that he did not find any). Oralia with 7-8 marginal spines, and 8-9 suboral ones, 3 of these conical and placed along the suture. Ventrolateral plates with granules.

Koehler (1921) records an additional specimen of this form taken by the Hirondelle II west of the Canary Islands (st. 3223: 30°50′N, 25°43′W, 5300 m).

Lieberkind (1935) concluded that *H.gracilis* was specifically identical with *H.parfaiti*.

Hyphalaster parfaiti is the name under which the more recent authors have recorded the Atlantic specimens of *Hyphalaster:*

Lieberkind (1932) recorded 14 and 12 specimens respectively from two Valdivia dredgings in the Gulf of Guinea (st. 56: 3°10′N, 5°28′E, 2278 m, blue mud, 3.3° C; and st. 63: 2°00′N, 8°04′E, 2492 m, 2.6° C.), ranging in size from R/r about 33/14 to 49/20 mm (e.g. 32/18, 34/14, 34/19, 37/16, 42/20, 43/19, 45/20, and 45/52 mm); number of superomarginals e.g. 13 by R 34 mm, 14 by R 41 mm, and 16 by R 47 mm; 7-9 cribriform organs.

Lieberkind (1935) further recorded *H.parfaiti* from two Ingolf dredgings: southeast of Greenland (st. 20: 58°20′N, 40°48′W, 3190 m, 1.5° C., 5 specimens), and in the southern Davis Strait (st. 37: 60°17′N, 54°05′W, 3230 m, 1.4° C., from which catch 30 specimens are present). The Ingolf specimens range in size from R/r 16/8 to 52/24 mm (e.g. 26/11, 26/13, 32/14, 38/17, and 45/19 mm); number of superomarginals e.g. 11 by R 26 mm, 14 by R 38 mm, 15 by R 46 mm, and 16 by R 43 mm; 7-9 cribriform organs.

A. H. Clark (1948) recorded 7 specimens of *H.parfaiti* taken by the Atlantis in the mid-North Atlantic (st. 15: 35°17′N, 30°51′W, 3200 m); R/r 17/7, 17/8, 27/11, 30/11, 33/14, 34/13, and 34/14 mm; 5-9 cribriform organs.

Madsen (1951) recorded the species from two dredgings of the Swedish Deep-Sea Expedition (on board the Swedish Albatross): In the tropical mid-Atlantic (st. 342: about 1°N, 18°40′W, 5250-5300 m, globigerina ooze, 2.3° C., 19 specimens), and in the tropical West-Atlantic (st. 357: about 2°25′N, 39°24′W, 4474-4430 m. calcareous clay, 1.3° C., 3 specimens). These specimens range in size from R/r 12/6 to 43/16 mm, (e.g. 12.5/6.5, 24/11, 32/11, and 32/14 mm), and have 5-11 cribriform organs. The smallest specimen has 6-7 superomarginalia.

The fairly large number of specimens available from some populations gave Lieberkind a fair knowledge of the infraspecific variation, and from this and a re-examination of several of the previously described specimens of *Hyphalaster,* he arrived at the conclusion – as already mentioned above – that all Atlantic specimens of *Hyphalaster* hitherto recorded, belonged to one and the same species, first described by Perrier in 1885 under the name of *Hyphalaster parfaiti*. LIEBERKIND (1935 p. 21) thus states: "Altogether the genus *Hyphalaster* seems to be a genus, in which the specific characters are rather vague; a thorough and critical revision not only of the forms from the Atlantic, but also of those from the Pacific is very desirable, but this is unfortunately beyond the scope of this work."

It is very regrettable that LIEBERKIND did not also discuss his material in relation to the forms of *Hyphalaster* described from the Pacific, so that it is unknown what characters, if any, he would consider of specific value in distinguishing between these different named forms. – The present author considers it impossible to distinguish the Atlantic *H. parfaiti* from Sladen's *H. inermis* from the Pacific, and the supposed vagueness of specific characters merely indicating that the various nominal species were described on the basis of characters of no specific value.

LIEBERKIND (1935) gave illustrations of the variations in shape of different specimens (different proportions of R to r was the main character for distinguishing some of the described "species"). He pointed out that the shape may vary a good deal in the individuals and that further the preservation is of some consequence. (As emphasized above the ratio R/r also always changes gradually with age due to the positive allometric growth of the arms, cf. the diagram fig. 4 p. 52).

LIEBERKIND (1935 p. 22) mentions that: "Papulae are only to be found in the distal part of the radial region of the paxillae area." Since, however, the papulae never occur in the actual radial lines, it is the distal part of the disk area to both sides of the radial lines which is meant. None of the previous authors had observed papulae in *Hyphalaster*.

The number of oral and suboral spines were found by LIEBERKIND to be very variable. In some of the specimens from off Greenland he found some "rather coarse granules which nearly resemble short spines" along the border of the marginal plates, and most numerous on those next to the extreme cribriform organ.

The Galathea material:

The Atlantic:

St. 24. 3°54′N, 8°22′W, 3200 m, 2.7°C., clay. 4 specimens.
St. 30. 0°42′N, 5°59′W, 5160 m, 2.2°C., clay. 17 specimens.
St. 52. 1°42′N, 7°51′W, 2550 m, ca. 3°C., muddy clay. 17 specimens.
St. 65. 2°17′S, 8°10′E, 2770 m, 3.0°C., bluish clay. 1 specimen.
St. 99. 8°40′S, 11°10′E, 2690 m, 3.9°C., yellowish clay. 5 specimens.

The Indian Ocean:

St. 186. 32°33′S, 32°01′E, 3620 m, 1.2°C., globigerina ooze. 1 specimen.
St. 192. 32°00′S, 32°41′E, 3530 m, 1.1°C., globigerina ooze. 1 specimen.
St. 193. 32°34′S, 31°52′E, 3680 m, 1.1°C., globigerina ooze. 12 specimens.
St. 234. 5°25′S, 47°09′E, 4820 m, 1.4°C., (globigerina ooze?). 1 specimen.
St. 238. 3°23′S, 44°04′E, 3960 m, 1.8°C., globigerina ooze. 12 specimens.
St. 280. 1°56′N, 77°05′E, 4350 m, 1.3°C., globigerina ooze. 2 specimens.
St. 281. 3°38′N, 78°15′E, 3310 m, 1.8°C., globigerina ooze. 1 specimen.
St. 282. 5°32′N, 78°41′E, 4040 m, 1.5°C., blackish mud. 32 specimens.

The Pacific:

St. 664. 36°34′S, 178°57′W, 4540 m, 1.1°C., brown sandy clay with pumice. 2 specimens.
St. 668. 36°23′S, 177°41′E, 2640 m, 2.0°C., clay. 1 specimen.

The Galathea material of *Hyphalaster inermis* from each of the three oceans is treated separately in the following, since the specimens hitherto recorded from the Atlantic and the Pacific were formerly regarded as representing several species. There can be no objection to the identifying of the present Atlantic specimens, all from the region of the Gulf of Guinea, with the form named *H. parfaiti* by LIEBERKIND, and the description of the materials from the Indian and the Pacific oceans thereafter will demonstrate the specific identity of the whole lot.

The Atlantic specimens. (Figs. 6*a-f, o, r, t;* 7*n, q-s, u-v*. Pl. I):

A total of 44 specimens of *Hyphalaster* s. str. were collected in the Atlantic. The four specimens from st. 24 have R/r 6/4, 12/6, 62/21, and 64/21 mm. The 17 specimens from st. 30 have R/r 7/4, 10/5, 14/7, 17/9, 19/11, 21/10, 22/11, 24/11, 25/11, 38/15, 40/20, 41/16, 43/20, 44/15, 44/19, 47/20, and 49/21 mm. Five of the 17 specimens from st. 52 have R/r 18/9, 21/11, 23/9, 29/10, and 32/12 mm, nine others have

R measuring from 38 to 49 mm, and three have R/r 60/20 mm. The single specimen from st. 65 has R/r: 48/18 mm. The five specimens from st. 99 have R/r 10/5, 18/9, 57/18, 58/21, and 59/19 mm.

The ratio R/r is less than 2 in the smallest specimens, 2 in those with R about 10-20 mm, and then on an average it gradually increases to 3 in the largest specimens, with R about 60 mm. As it will appear from the measurements recorded, and from the accompanying photos pl. I, the ratio R/r may be very varying in otherwise equal-sized specimens.

The numbers of superomarginal plates and of cribriform organs are the following:

R	Number of superomarginals	Number of cribriform organs
6-7 mm	3-4	3-5
10 mm	6-7	5-7
12 mm	7-8	7
14 mm	8-9	8-11
17-18 mm	9-10	7-9
19-24 mm	11	9-11
25-29 mm	12-13	7-9
32-41 mm	14	7-11
43-49 mm	14-15	7-11
48-57 mm	17	7-11
58-62 mm	17-18	7-9
64 mm	19	9

The superomarginal plates in general join those of the opposite side of the arms from nos. 5-6. In the two smallest specimens, R/r 6/4 mm (fig. 6*a-c*) and 7/4 mm (pl. I, 13), with still only 3-4 superomarginals, these are then separated for the whole length of the arms. In the population from st. 30 also the sixth pair of opposite superomarginals tend to remain separate, and actually the opposite superomarginals in some arms of these specimens do not meet until plates no. 7. The superomarginals thus remain separate to the terminal ossicle in a specimen with R/r 10/5 mm (pl. I, 11), although 6-7 superomarginal plates are present; and a single specimen, R/r 24/11 mm, is remarkable in having the superomarginals separate in some arms as far as to the 7th or 8th pair of plates. (Pl. I, 5).

The superomarginal plates of either side of the arms in general correspond exactly with each other, but they may also alternate to a varying degree, and they may be differently arranged in the different arms of the same specimen. One, or more often two superomarginal plates are situated below the terminal ossicle, and are hence triangular. The superomarginals of the disk are subquadrate, or, in large specimens, somewhat longer than high. The more distal of the superomarginals may be higher than long, often markedly so in the small specimens, less pronouncedly in the large ones. Koehler (op. cit.) described the proximal (disk) superomarginals of his specimens of *H. fortis* and *H. gracilis* as much higher than long, but this may be due to the fact that he has only considered the naked surface of the plates, and disregarded the parts covered by the cribriform organs. The superomarginals of the arms sometimes have the proximal margin slightly concave and the distal margin correspondingly excave, so that the vertical sutures appear as curved lines with the concavity directed towards the tip of the arms (fig. 6*t*).

The inferomarginal plates typically lie exactly below their superomarginal companions, but may also subalternate with these. They are of the same number as the superomarginals, or maybe one or two more. The small specimen from st. 30, with R/r 7/4 mm, has up to 5 inferomarginals together with 3-4 superomarginals. The inferomarginals are in the proximal part of the arms slightly lower than their superomarginal companions, but towards the end of the arm they decrease relatively more in height than do these, and distally the difference in height thus becomes more pronounced.

A few specimens have proximally in the midline of one or more of the arms, for a stretch of up to 3 superomarginals, a series of small rounded secondary plates, e.g. two specimens from st. 52 with R. 18 and 45 mm, and two specimens from st. 30 with R. 19 and 49 mm. (Fig. 6*t*).

The most proximal marginal arm plates in the large specimens may carry some granular spinelets along the vertical margins, especially along the aboral one. Generally, however, the plates are completely naked (except for the papillae of the cribriform organs).

The cribriform organs are only just developed in the juvenile specimen with R/r 6/4 mm (st. 24). The largest number is here 3 in each interradius, and they are most distinct in the interradius with the madreporite, whereas they are hardly discernible in the other interradii, being quite rudimentary, with only a single series of papillae to each side of the vertical sutures, and not yet extending the whole way to the ventral side (figs. 6*a-b*). In the specimen with R/r 7/4 mm (st. 30) there are 3-5 cribriform organs in each interradius, also yet all rudimentary. In the two specimens with R/r 10/5 mm, the number of cribriform organs is 5 in that from

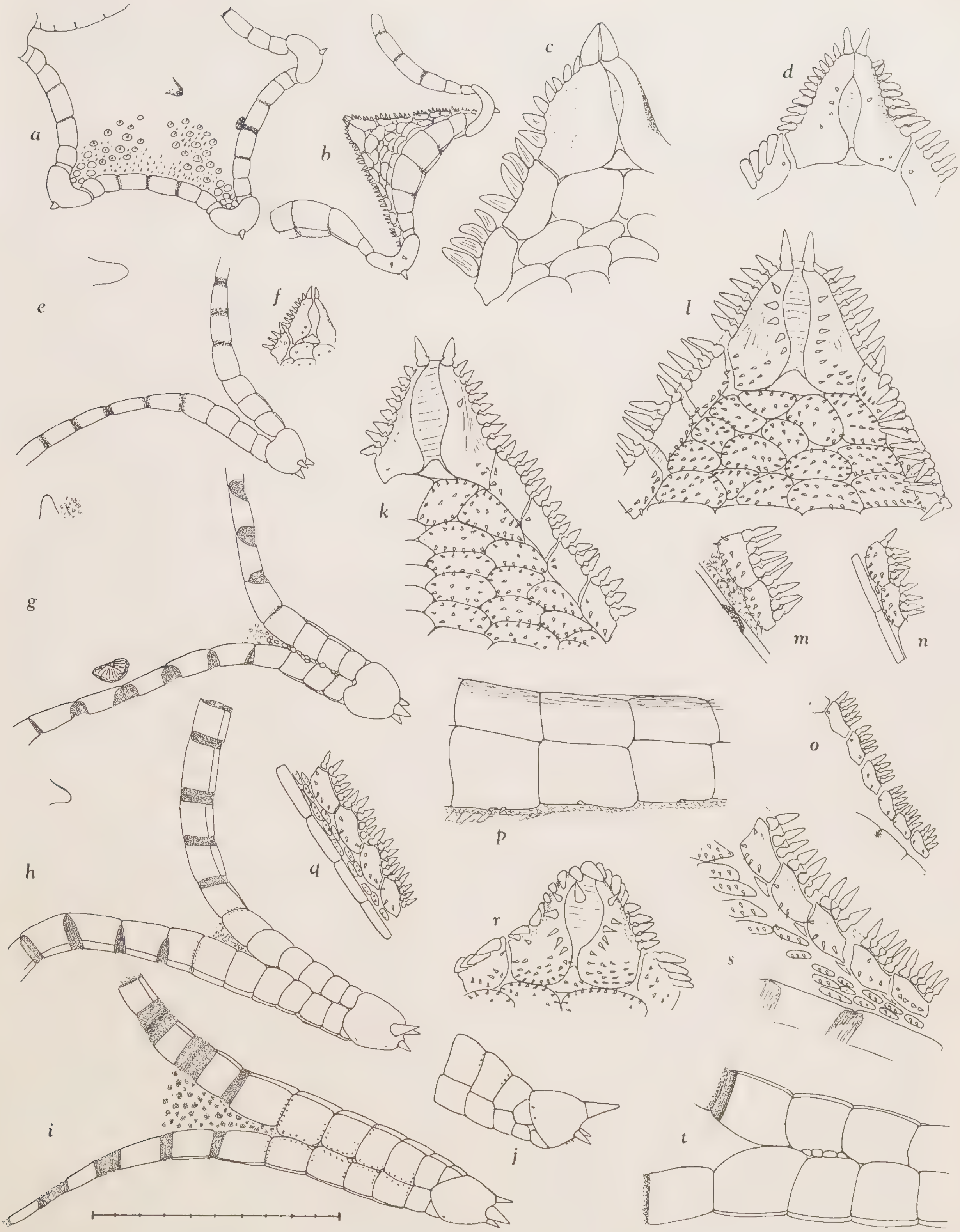


Fig. 6. *Hyphalaster inermis.* a-c) St. 24, R/r 6/4 mm; a, dorsal view; b, ventral view; c, jaw in four times larger scale. d) St. 30, R/r 14/7 mm, jaw (in twice the usual scale). e-f) St. 24, R/r 12/6 mm, part of dorsal side and jaw. g) St. 280, R/r 16/8 mm, (see also fig. 7o). h) St. 192, R/r 17/6 mm. i-j) St. 282, R/r ab. 20/11.5 mm, same arm in dorsal view and from the side, (see also fig. 7f). k) St. 282, R/r 48/15 mm, part of ventral side. l-n) St. 238, R/r ab. 53/21 mm; l, part of ventral side; m, adambulacralia nos. 8-9; n, adambulacralia nos. 17-18, inferomarginalia nos. 10-11, (see also fig. 7g, h, p). o) St. 99, R/r 18/9 mm, adambulacralia nos. 1-6. p) St. 234, R/r 75/21 mm, marginals nos. 10-12 in side view. q) St. 238, R/r 46/16 mm, adambulacralia nos. 15-18. r) St. 99, R/r 57/18 mm, jaw, (see also fig. 7q). s) St. 238, R/r ab. 44/19 mm, part of ventral side with the adambulacralia nos. 4-8. t) St. 30, R/r 49/21 mm, basal part of arm in dorsal view.
Scale: 10 mm (in d 5 mm, in c 2.5 mm).

st. 99, and 7, the outermost ones rudimentary though, in that from st. 30. In all larger specimens there are in each interradius from 7 to 11 cribriform organs. The number is often somewhat varying in the different interradii of the same specimen, and may be unequal to each side of the median organ (thus there may be 8 or 10 cribriform organs in the interbrachial series).

The cribriform organs are generally developed from the dorsal side, and the rudimentary ones therefore yet solely occupy the superomarginal sutures. Full-grown specimens have at least 7 cribriform organs; and 7 cribriform organs only are also found in some of the largest specimens, with R up to 58 mm, while 11 cribriform organs are found in some interradii of a specimen from st. 52 with R 50 mm, in all interradii of the specimen from st. 65 with R 48 mm, and in about two-thirds of the specimens from st. 30. In this latter population even a specimen so small as with R/r 14/7 mm shows in some interradii 11 cribriform organs (the outer ones, however, still rudimentary). One specimen with R/r 49/9 mm also shows a twelwth, rudimentary cribriform organ in one interradius. The remaining specimens from st. 30 all have 9 cribriform organs in each interradius. The large number of cribriform organs in the population from st. 30 is connected with a tendency of the superomarginal plates to remain separate for a longer distance than is usual in the other specimens at hand (the disk thus being relatively larger).

The large cribriform organs are in general composed of up to 16 rows of papillae. In the specimens from st. 30 there may be even 22 rows of papillae, and in these specimens successive cribriform organs are often in contact. The structure of the cribriform organ is papilliform, with the calcareous papillae slender and flattened. Those of the outer covering series are not much larger than the other ones. The series of covering papillae extend in a continuous series from one dorsal corner of the organ to the other dorsal corner, so that the cribriform organs typically are well marked off ventrally. In large specimens, however, the median cribriform organ, which becomes gradually larger with age, may appear indistinctly marked off also ventrally, where it adjoins the spinulated ventral disk area.

The terminal ossicle is rather conspicuous in the juvenile specimens, broad, and with the adoral dorsal margin concave, in connection with the dorsal integument here reaching to it between the opposite superomarginals (fig. 6*a*). It carries 3 spines, a distal terminal one and a pair of subterminal ones, which latter apparently are not yet developed on some of the terminal ossicles of the smallest specimen at hand, with R 6 mm. In the somewhat larger specimens (in which the distal superomarginals encase the arms) the terminal ossicles become more elongate, oval in outline, when seen from above, and placed slightly dorsal to the end of the arms, covering one or usually two rudimentary superomarginals. In medium-sized specimens the terminal ossicles are still rather prominent, but in the largest specimens they become fairly inconspicuous, being here flush with the superomarginals of the arm end. As a rule the terminal ossicles, also in the largest specimens, bear only 3 fairly short and conical spines (the unpaired terminal one and the pair of subterminal ones), but large specimens exceptionally may have two pairs of subterminal spines.

The whole dorsal side of the disk is armed with a close pavement of fairly uniform small paxillae with rather granular spinelets. (Fig. 7*n*, *q-s*, *u-v*). Embryonic plates are still discernible radially in the juvenile specimens with R about 6-7 mm (fig. 6*a*), but are in the state of being absorbed, and with paxillar shafts developing centrally upon them. And the paxillae covering the central and interradial areas are yet with only single spinelets. In the juvenile specimen with R/r 10/5 mm the paxillae carry 1, 2, or 3 spinelets.

The average number of spinelets on the paxillae, as well as the largest number found, varies considerably in the different specimens. In specimens with R about 20 mm, the largest number of paxillar spinelets ranges from 6 to 12 in different individuals; in specimens with R about 30 mm it ranges from 15 to 18, in those with R about 40 mm from about 15 to about 20. In the larger specimens the maximal number of spinelets on the paxillae varies generally from about 15 to about 20, and is exceptionally about 30. In the two large specimens from st. 24, with R 62 and 64 mm, the average number of spinelets on the paxillae is about 12 and 16 respectively, with 2-4 central spinelets surrounded by a circle of peripheral ones; and the largest number of spinelets counted is 18 and about 25 respectively. Incidentally, these two large specimens from st. 24 correspond closely in size and in number of superomarginals (18-19) to those described by KOEHLER (1907) under the name of *H. fortis*, the paxillae of which, however, were stated to have about 10 central granules surrounded by a circle of peripheral ones. Such large paxillae with e.g. 13 central spinelets surrounded by a circle of 17 peripheral ones, are in the present material only observed in a specimen from st. 99 with R/r 58/21 mm and 17 superomarginals. The paxillae are all more or less circular (to polygonal) in contour. They are all about subequal in height, the larger ones being about as wide as high, and the smaller ones correspondingly more slender. The paxillar shafts show a distinct constriction which marks off the basal part, imbedded in the integument. (Fig. 7*r*).

Papulae have been observed in some specimens (fig. 7*s*), also fairly close to the center of the disk.

An apical appendage, or at least an apical cone, is usually distinct in the small specimens. An apical appendage may be present also in medium-sized specimens, and an apical cone may be found in specimens as large as with R up to 64 mm. Several large specimens, and also a few smaller ones, however, do not show any apical prominence at all. They usually have the central area provided with paxillae of a distinctly smaller size than those of the main part of the disk, but even such a difference in the armature of paxillae is not always present.

The madreporite is roundish or more or less distinctly tangentially elongate, perhaps kidney-shaped with the concave side adcentrally directed. In grown-up specimens its diameter is slightly less than the length of the adjoining marginals, but in the juveniles it is relatively smaller. It may lie close to the marginal plates, but usually it is separated from these by one or three (4) rows of paxillae. Its striae radiate from a point situated eccentrically near the adcentral margin.

The adambulacral ossicles of the disk are rather subrhomboid in contour, whereas those in the free arms are rather subcrescentic. Each ossicle bears along the furrow a series of 4-5 subequal and uniformly spaced spines (exceptionally, on some of the proximal ossicles in a large specimen, there are 6 furrow spines). The furrow spines are rather spearhead-shaped (lanceolate), with a constriction in their lower part, marking the extension of the connecting web, and their outer part more or less distinctly flattened in vertical direction, subquadrangular or subtriangular in cross-section, and with a blunt end. On the surface of the adambulacral ossicles there are a few subambulacral spinelets, in small specimens e.g. often a minute one on the adoral part of the ossicle, and a slightly larger one aborally, while in large specimens there may be up to 5 subambulacral spinelets in a longitudinal series, and on the most proximal plates in addition a few more spinelets between this series and the furrow edge, especially on the adoral part of the ossicle.

The number of adambulacral ossicles is e.g. 7-8 in a specimen with R 6 mm and 3-4 superomarginals, 13 in one with R 10 mm and 6-7 superomarginals, 17 in one with R 18 mm and 9 superomarginals, 27 in one with R 48 mm and 17 superomarginals, and 27 too in one with R 57 mm and also 17 superomarginals.

The oral ossicles (fig. 6*c, d, r*) bear along their margin a series of on an average 8 oral spines, the number usually varying from 7 to 9, occasionally being 10, and exceptionally 11-12. A specimen with R/r only 14/7 mm thus has 12 oral spines on one of the oralia, whereas the others bear 9-10 such spines. The oral spines are shaped like the adambulacral ones.

The surface of the oral ossicles is naked in the juvenile specimens at hand, but in the larger specimens there is always a varying number of suboral spinelets and spines. A specimen with R 10 mm thus is provided with a couple of suboral spinelets; and medium-sized specimens usually have a few conical spines on the protruding part along the suture and a varying number of spinelets on the distal surface. In the large specimens there may be up to 6 small conical suboral spines in a series along the suture, and up to 10 suboral spinelets distally.

The primary oral ossicle is well exposed, showing a triangular surface, and is often provided with a few spinelets.

The ventrolateral area is armed with a pavement of plates, which slightly overlap in adoral direction. In the juvenile specimens these plates are arranged in about 4 tangential rows, in the medium-sized specimens in about 10, and in the largest specimens in up to 12-13 of such rows. Twelve is the usual maximum of tangential rows of ventrolateral plates, and the number may vary in different interradii. The ventrolateral plates are further arranged in radiating series, two and two corresponding with one adjoining marginal plate. The proximal and largest ventrolateral plates are irregularly shaped, whereas the more distal ones are transversely elongate or subhexagonal. Minute ventrolateral plates extend somewhat along the free arms, e.g. about half their length in a specimen with R 48 mm and 17 superomarginal plates. The ventrolateral plates are still naked in the juvenile specimens with R less than 10 mm, but otherwise they bear a fairly uniformly spaced armature of spinelets, on the proximal larger plates generally placed along the adoral border (e. g. in a number of about a dozen, or a little more, to a plate) on the more distal plates arranged in one or two median series, parallel to the long sides.

Some specimens are seen covered with a thick, deciduous skin.

The Indian Ocean specimens. (Figs. 6*g-n, p-q, s;* 7*a-m, o-p, w-æ*. Pls. II-III):

The Galathea Expedition collected a total of 62 specimens of *Hyphalaster inermis* in the Indian Ocean, viz. 14 specimens in three dredgings near Durban (sts. 186, 192, 193), 13 specimens in two dredgings near Mombasa (sts. 234, 238), and 35 specimens in three dredgings near Ceylon (sts. 280, 281, 282). As was to be expected, this additional large material somewhat enlarges the infraspecific variation known.

The single specimen from st. 186 has R/r 33/14 mm, and that from st. 192 R/r 17/6 mm. The twelve specimens from st. 193 have R/r respectively 18/8, 24/10, 26/10, ?/11, 31/12, 32/12, 32/13, 33/12, 33/12, 34/13, 34/14, and 36/12 mm. The single specimen from st. 234 has R/r 75/21 mm, and the twelve specimens from st. 238 have R/r 39/15, 44/19, ?/19, 46/16, 53/20, 53/21, 58/20, 60/18, 62/20, 65/21, 70/20, and 70/22 mm. The two specimens from st. 280 have R/r 16/8 and 59/18 mm, that from st. 281 has R/r 45/14 mm, and the thirty-two from st. 282 have R/r 20/11, 33/13, 36/14, 38/13, 43/14, 48/15, ?/17, 56/19, 58/18, 62/18, 62/21, 62/22, 63/20, 64/20, 65/18, 67/20, 67/20, 67/21, 68/22, 68/22, 69/22, 70/21, 70/21, 70/21, 70/25, 72/24, 74/19, 74/20, 74/23, 75/23, 75/24, and 80/24 mm.

Several of these specimens from the Indian Ocean are thus distinctly larger than anyone known from the Atlantic. The ratio R/r varies from about 2 in the smallest specimen at hand up to about 3 in specimens with R about 60 mm (which corresponds to the largest Atlantic specimens hitherto known) and increases (in conformity with the positive allometric growth of the arms) to about 3.5 in specimens with R about 70-80 mm or more, exceptionally to almost 4, as in a specimen with R/r 74/19 mm.

The numbers of superomarginal plates and cribriform organs are as follows:

R	Number of supermarginals	Number of cribriform organs
16 mm	7-8	(5)-7
17-18 mm	9	(5)-7
20-34 mm	10	7-9
20-33 mm	11	7-9
26-34 mm	12	7-9
32-39 mm	13	7-11
36-39 mm	14	7-11
36-58 mm	15	9-11
43-67 mm	16	9-11
58-70 mm	17	9-11(-13)
59-72 mm	18	9-11
59-75 mm	19	9-11(-19)
62-80 mm	20	9-13
62-75 mm	21(-22)	11-15

Eleven cribriform organs in each interradius is the usual maximum, but 13 to an interradius occur in three specimens with R 58, 62, and 70 mm, and 17, 20-22, and 17-21 superomarginals respectively. Fifteen cribriform organs are found in the interradii of a specimen with R/r 74/19 mm and 21 superomarginals. The extraordinarily large number of 17-19 cribriform organs to an interradius is found in a specimen with R/r 67/20 mm and 19 superomarginals (pl. III 1). The largest number of superomarginals, 22, is found in a specimen with R/r 62/18 mm.

The superomarginals in general join their opposites in the midline of the arms from the fifth or sixth pair, or, more rarely, from the seventh pair. In the present material the joining of the superomarginals may, however, take place both more proximally as well as more distally. In a specimen from st. 193 with R/r 31/12 mm the fourth superomarginal plates thus meet their opposites for a distance of their length in all five arms, and in another specimen from the same haul, R/r 26/10 mm, they do so in some of the arms. In the available twelve specimens from this population from st. 193, the disk is upon the whole relatively small, the superomarginals as a rule meeting their opposites from no. 5. In the population from st. 282, represented by 32 specimens most of which are large ones, the disk area on the other hand is in general relatively large; the opposite superomarginals here usually join from the sixth or seventh plates, and in a few specimens, with R/r 64/20, 67/20, 70/21, and 74/19 mm, they at least in some arms do not join until plates no. 8. In the specimen with R/r 67/20 mm (pl. III 1) the seventh pair of opposite superomarginals are separated in all the arms by 2-3 rows of paxillae, and in one arm a single row of paxillae also separates the eighth pair of superomarginals in their whole

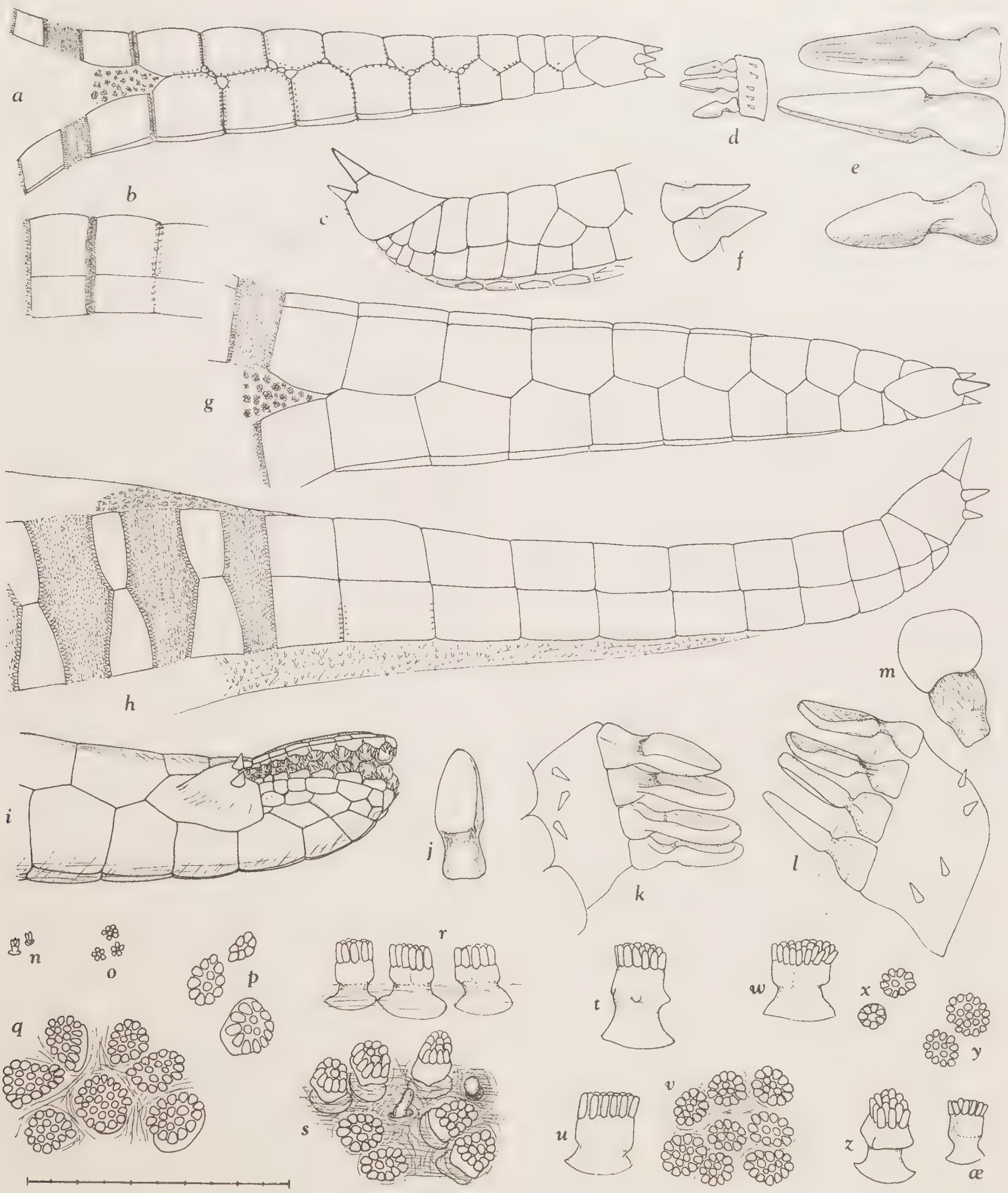


Fig. 7. *Hyphalaster inermis*. a-b) St. 282, R/r 43/14 mm; a, arm in dorsal view, first joining superomarginals are nos. 6; b, marginals nos. 5-7 in lateral view. c) St. 282, R/r 62/18 mm, (see also w-æ). d-e) St. 282, R/r 74/19 mm; d, adambulacral ossicle no. 6; e, same spines in four times larger scale. f) St. 282, R/r about 20/11 mm, oral spines, (see also fig. 6 i-j). g-h) St. 238, R/r about 53/21 mm, arm in dorsal view and in lateral view, (see also p and fig. 6 l-n). i) St. 282, R/r 67/20 mm, abnormal arm end. j-k) St. 193, R/r 36/12 mm; j, furrow spine seen from the adoral side; k, adambulacral ossicle no. 4. l-m) St. 193, R/r ?/11 mm; l, adambulacral ossicle no. 4; m, furrow spine from the adambulacral ossicle no. 1 seen from the adoral side. n-æ) Dorsal paxillae; n, st. 24, R/r 12/6 mm; o, st. 280, R/r 16/8 mm; p, st. 238, R/r ab. 53/21 mm; q, st. 99, R/r 57/18 mm; r-s, st. 24, R/r 64/21 mm; r, three paxillae in side view; s, a group of paxillae in dorsal view and with a few papulae observable; t, st. 282, R/r 64/20 mm; u-v, st. 24, R/r 64/21 mm; w-æ, st. 282, R/r 62/18 mm. Scale: 10 mm in a-d and g-i, 2.5 mm in e-f and j-æ.

length (this specimen with the unusually large disk area is also the one with the exceptionally large number of up to 17-19 cribriform organs in each interradius). In the population from st. 282, however, also a specimen as large as with R/r 74/20 mm (pl. III 2) may be found with the opposite superomarginals no. 5 meeting, at least in part.

The superomarginals as usual often subalternate to a varying degree, also in different arms of the same specimen. The regular quadrangular appearance of the plates may be completely lost in some arms, in which especially the superomarginal series may be broken up into triangular or irregularly polygonal plates. The superomarginals sometimes appear very slightly tumid, which may give the arm a somewhat annulated appearance (fig. 6*g*-*h*) as was described by SLADEN (1883 p. 240) for the type-specimen of *H. inermis*. The Indian Ocean material likewise includes some specimens in which a varying number of small rounded supplementary plates are inserted between the otherwise joining superomarginals (fig. 7*a*), generally only in the proximal part of the arms, but occasionally almost to the terminal ossicle. In one specimen from st. 282, R/r 74/23 mm, such plates occur in an almost continuous row for a distance of six succeeding superomarginals. About one-fifth of the specimens from st. 282 have secondary dorsal arm plates.

In the smallest specimen in this material, one from st. 280 with R/r 16/18 mm (fig. 6*g*), the fourth and fifth pairs of superomarginals are separated by a series of small rounded plates, in appearance similar to the secondary dorsal arm plates of the large specimens, but in the present case probably to be interpreted as embryonic plates which have not yet been replaced by the paxillae of the full-grown individual. Nor are the paxillae of the arm bases in this specimen fully developed, having only a few spinelets on the paxillar shafts which are formed on the not yet completely absorbed embryonic plates.

In the specimens with R less than about 35 mm, the arm plates are generally naked, whereas in the larger specimens they often bear some minute granules or granuliform spinelets, as was also the case in a few of the largest specimens from the tropical East Atlantic, described above, and in some of the Greenland specimens described by LIEBERKIND (1935). The marginal granuliform spinelets appear to be so easily lost that a description of their distribution may often be very uncertain. Where best developed, this armature of spinelets is found as a single series all way round along the margins of the arm plates, and thus at the vertical sutures gives the impression of a rudimentary cribriform organ with yet only two series of papillae. The marginal spinelets, however, are in general confined to the more proximal arm plates, though in some specimens they may occur to the arm end. In many specimens they are developed only along the aboral vertical margins (of the inferomarginal as well as of the superomarginal plates). In others they are developed also along the adoral vertical margins (here always being of a smaller size) and along the ventral margin of the superomarginals. Only more rarely do they occur also along the dorsal margin of the inferomarginals, and only rather exceptionally do they form the continuous series all around along the margins of both superomarginal and inferomarginal plates.

Some of the inferomarginals of the arms in the single specimen from st. 234, R/r 75/21 mm, bear medially near the ventral margin one or a few spinelets (or minute spines), slightly larger than the neighbouring ventrolateral spinelets (fig. 6*p*). It is probably a character attained with age, but is not seen in any of the other specimens at hand.

The arms of the larger specimens of *Hyphalaster* apparently are frequently subject to damage in the living animal, since in the present material several specimens are observed with arms in different stages of regeneration. One specimen from st. 282, with R/r 56/19 mm and 16 superomarginals, has once lost an entire arm, and the wound has then healed by the marginal plates closing over it, so that the specimen now appears with an almost regularly quadrate disk with an arm extending from each corner (pl. XIII 4). Probably also the peculiar abnormality to be described on p. 69, of the arm ends being bent back and fused with the more proximal part, is to be assigned to a regeneration after an injury. The specimen from st. 234 with R/r 75/21 mm has the single preserved arm furnished with two terminal ossicles, one above the other, and also this may be due to an irregular regeneration.

The number of cribriform organs by different lengths of R has been recorded above. The largest of the specimens at hand, R/r 80/24 mm, has 13 cribriform organs in some interradii, and 12 in the others. The specimen with R/r 67/20 mm and 19 superomarginals, which meet from pairs no. 8 (pl. III 1) has in each interradius 13-15 fully developed cribriform organs, reaching from the dorsal to the ventral side of the disk, and to each side of this series two additional, rudimentary ones. The specimen thus shows the unusual feature of having cribriform organs formed also around the vertical suture of a set of marginal plates belonging to the arm. The rudimentary organs are best developed at the horizontal suture, the proximal one reaching to the ventral but not to the dorsal side of the disk, and the distal one, with up to 6 rows of papillae, reaching only to about the middle of either series of marginals.

The largest cribriform organs comprise up to about 24 series of papillae, and in some specimens the median ones merge in part with their neighbours at the dorsal edge of the marginals and possibly also at the horizontal suture. In a specimen with R/r 70/21 mm and 13-14 cribriform organs, the 9-11 median ones thus are in contact medially, at the horizontal marginal suture, and dorsally close to the disk, thus leaving free only a triangular patch on the lower part of the inferomarginals, and a diamond-shaped patch on the median part of the superomarginals. Usually, however, the cribriform organs are well separated.

The terminal ossicles carry also in the large specimens of the present material typically 3 fairly short spines. (In some of the larger specimens it looks as if the terminal spines have been worn down in the living animal, which cannot be stated with certainty, however, since these spines are so easily lost, and thus may have been lost during dredging or later during the handling of the specimens). Sometimes, but rarely, there are two pairs of subterminal spines, thus 5 terminal spines in all. The terminal ossicle may be rather conspicuous also in some of the largest specimens at hand.

One specimen from st. 282, R/r 67/20 mm, shows a peculiar abnormality in two of the four arms preserved. The distal arm end is bent up and backwards for a length of about 1 cm and coalesced with the dorsal side of the arm (fig. 7*i*, pl. XIII 3), the outermost part of the ambulacral furrow thus being dorsal to the arm end, and the terminal ossicle becoming pushed in between the opposite superomarginals as a triangular "plate", its adoral end (the distal end of the normal ossicle) being low and flush with the superomarginals, while the aboral end is elevated and bears a pair of spines (the subterminal ones, whereas no trace is found of the distal terminal spine).

The largest paxillae bear in the specimens with R up to about 40 mm, from 10 to about 15 (exceptionally 20) spinelets. In specimens with R 60 mm or more, the largest paxillae carry from about 10-12 to 20-25 spinelets (fig. 7*p*, *w-æ*), sometimes, as in the specimen with R 80 mm, even up to about 30 spinelets. The specimen from st. 234, with R/r 75/21 mm, e.g. has the paxillae provided with from about 6 to 12 spinelets, in the small paxillae in a circular crown, in the large ones with a central spinelet surrounded by a circle of peripheral ones.

Papulae are as usual in the porcellanasterids rarely observable. In the specimens in which they are seen they are present in a slightly larger number than the paxillae, each paxillae e.g. being surrounded by 5-6 papulae, and each papula being found in the space between three adjoining paxillae.

A short apical appendage is present in some of the small specimens, and in the others there is an apical cone. An apical cone is often present in the large specimens too, thus also – though a very low one – in the largest specimen, with R 80 mm. Otherwise there is in the large specimens merely a small central area with smaller paxillae.

The madreporite shows no deviations from the appearances found in the Atlantic material described.

The adambulacral armature (fig. 6*k-n, q, s*) is as a rule as described for the Atlantic material, with 4-5 subequal lanceolate furrow spines, and some spinelets in an irregular row along the interradial margin of the adambulacral ossicles; but the number of furrow spines may vary from 3 to 6, and there may be only a single (or perhaps none) subambulacral spinelet. A few specimens with R ranging from 39 to 74 mm thus have only 3 furrow spines on some or on most of the adambulacral ossicles of the disk area, whereas the adambulacral ossicles in the arms usually have 4-5 furrow spines. As a general rule the adambulacral ossicles of the free arms have either the same number of furrow spines as those of the disk, or one more, and the few ossicles found with 6 furrow spines therefore always belonged to the free arms of fairly large specimens, R 58-74 mm.

The furrow spines are generally spearhead-shaped (fig. 7*e*) with a conical basal part, a constriction to where the web connecting them reaches, and a longer obtusely pointed distal part which is flattened in a direction vertical to the furrow (in cross-section being subrectangular, subtriangular, or subcrescentic). In about one-third of the specimens from st. 193 (R 30-36 mm) however, all the furrow spines, and also the oral spines, have the distal part much broader, thus assuming the appearance of a handmirror (fig. 7*l-m;* pl. III 4). The ventral appearance of these specimens becomes very characteristic through this feature, but it is evident that it is only an individual variation, since the other specimens of the same population are provided with furrow spines of the usual spear-head shape (fig. 7*j-k;* pl. III 3) or, in one case, of an intermediate shape.

The subambulacral armature is best developed on the ossicles of the proximal part of the free arms, on which there may be about ten spinelets arranged in two irregular longitudinal series. In small specimens, the adambulacral ossicles of the disk area may sometimes have yet only a single, always adorally placed spinelet developed on their surface, so also a specimen with R 48 mm from st. 282 (in which some ossicles even appear completely naked); and specimens as large as R 70 mm may have only a couple of subambulacral spinelets. In the young specimens the subambulacral spinelets may appear relatively larger than in the older ones.

The number of adambulacral ossicles in relation to the size of the specimens and the number of superomarginal plates appears from the following examples:

R	Number of superomarginalia	Number of adambulacralia
16 mm	7-8	13
17 mm	9	17
20 mm	10-11	17
33 mm	12	21
38-46 mm	14-16	24-26
48 mm	16-17	27-29
53-60 mm	14-19	27-32
62 mm	20	33-34
64-70 mm	17-21	32-35
74 mm	19-21	36-38
80 mm	20	34

In fairly expanded specimens the end of the ambulacral ossicles may be seen between the adambulacral ones also in the proximal part of the arms.

The oral ossicles (fig. 6*k-l*) generally carry 7 or 8 marginal spines, of which the proximal one is about twice as large as the others. Exceptionally some oralia bear only 6 marginal spines, and other oralia may be found with 9 or even 10 marginal spines. Ten marginal oral spines are thus found in the large specimen with R 80 mm (the number of oral spines here varying from 8 to 10) as well as in a specimen with R only 17 mm.

The suboral armature consists of a varying number (up to about half a dozen) of short conical spines along the sutural margin, and further of a varying number of spinelets on the distal part of the ossicle. In the small specimens there may still be only a few spinelets. In the large specimens a suboral armature is usually well developed; and the proximal of the spines at the sutural margin may attain a length subequal to that of the large proximal oral spine, so that the pair of oralia forming a jaw, seems to be provided with a small cluster of mouth-spines. (Sometimes the suboral spines are found not on the oral ossicles proper, but on the skin extending over the suture. This must be due to an abnormal turning of the oralia in the preserved specimens and a contraction of the integument).

The marginal oral spines are – like the adambulacral ones – typically spearhead-shaped, as was also the case in the Atlantic material. In 3 of the 12 specimens from st. 193 they are, however, (like the adambulacral spines here) much broader, hand-mirror- or shovel-shaped, whereas they are of an intermediate appearance in a fourth specimen.

The primary oral ossicle may occasionally be armed with a few spinelets, as was also to be observed in some Atlantic specimens. One specimen from st. 282, with R about 68 mm, has all the primary oral ossicles provided with a number of spinelets similar to those occurring on the ventrolateral plates. Another specimen from the same population, with R/r 70/21 mm, has minute spinules on one of these ossicles, whereas the four others are bare.

The ventrolateral plates are in the present large specimens arranged in from 12 to 14, exceptionally up to 16 tangential rows, and 14 such rows are e. g. also found in a specimen with R only 58 mm. Small ventrolateral plates often extend in a narrow strip almost to the end of the arms. When the integument is preserved, the ventral area with the rather uniform covering of spinelets has a velvet-like appearance. Fairly distinct radiating spineless ridges often extend between the double radial rows of ventrolateral plates, from the adambulacralia to the marginal sutures.

Notes on the Pacific specimens:

The Galathea Expedition also collected a few specimens of *Hyphalaster inermis* in two dredgings in the Kermadec Trench north of New Zealand (sts. 664 and 668).

The two specimens from st. 664 have R/r 62/20 and about 23/9 mm respectively, (the latter specimen is very damaged). The one from st. 668 has R/r 13/5 mm.

The specimen with R/r 62/20 mm has 21 superomarginals, which join from nos. 7(-8), and 12-13 cribriform organs of which some may coalesce at the horizontal suture. That with R/r about 23/9 mm has 13-14 superomarginals (a rather high number), which join from nos. 6(-7), and 9-11 cribriform organs. The other with R/r 13/5 mm has 8 superomarginals which join from no. 5, and 9 (+ 2 rudimentary) cribriform organs. The marginals of the arms are naked in all the specimens. The terminal ossicles bear 3 spines.

The paxillae carry 9-18 spinelets in the large specimen, up to 8 spinelets in the medium-sized one, and 2-5 spinelets in the small one. The madreporite in the large specimen e.g., is transversely oval with the furrows radiating from an adcentral point. There is a short apical appendage in the small specimen, and a distinct apical cone in the medium-sized one.

The ambulacral armature consists proximally in the large specimen of 4 furrow spines and about 3 subambulacral spinelets, and in the arms of 4-5 furrow spines and 4-5 subambulacral spinelets. The same applies to the medium-sized specimen. In the small specimen there are 3(-4) furrow spines and a couple of subambulacral spinelets, which here appear relatively larger than in the other specimens. The number of adambulacral ossicles in the specimens is 32, 21, and 12 respectively.

The oral armature consists in the large specimen of 7 marginal spines and about 3 suboral ones along the suture, besides up to 5 spinelets on the distal surface. The medium-sized specimen has 7 marginal spines (on one ossicle 8), and 2 suboral ones at the suture and about 4 suboral spinelets distally. The small specimen has 7-8 marginal spines, and suborally 2 small spines at the suture and a single spinelet distally.

The ventrolateral plates are arranged in 14-15, 10-11, and 5 tangential rows respectively. In the two larger specimens they carry 5-9, in the small one up to 5 granuliform spinelets. In the large specimen the ventrolateral plates extend almost to the end of the arms, to the inferomarginals no. 18.

Biological remarks:

The stomach content of these specimens of *Hyphalaster* is the usual mud, presumably rich in bacteria, and with foraminiferans and various other organic items. A small twig, 23 mm long and 1 mm thick, was e. g. removed from the stomach of a specimen from st. 282 with R abot 65 mm.

A few eggs, 0.5-0.6 mm large, were found in the otherwise almost emptied gonads of a fairly large specimen from st. 238.

Ascothoracids were found in two specimens from st. 282 and in one from st. 52. Another specimen, from st. 30, shows a large calcified tumor ventrally, which probably also indicates the presence of an ascothoracid parasite. Larvae in the cypris-stage were found attached to the dorsal side of one of the specimens from st. 282.

Myzostoma specimens were found on three medium-sized specimens from st. 52, and on a large one from st. 282. They were found attached to the dorsal side, to the marginal plates, as well as to the ventral side.

Discussion:

All the 109 specimens of *Hyphalaster* s.str. collected by the Galathea Expedition in a total of 15 different dredgings, scattered over the tropical eastern Atlantic, the Indian Ocean, and the south-eastern Pacific, shall have to be grouped in a single species, as is evident from the descriptions given above. The study of the present material has confirmed that LIEBERKIND was right in considering all the hitherto recorded Atlantic specimens of *Hyphalaster* as of one species only *(H. parfaiti* Perrier, 1885), but it has further led to the conclusion that this species is the same as the *H. inermis* described by SLADEN in 1883 on specimens from off Japan.

SLADEN states in the original description of *H. inermis* that "The adambulacral plates join up to the infero-marginal plates along the whole length of the free portion of the ray, and there is consequently no extension of the interbrachial area along the ray". As described above, ventrolateral plates have been found extending a varying distance down the free arms of the examined larger specimens, but the feature is in part one of age, and smaller specimens of e. g. the same size as the type-specimen, R about 20 mm, may have the ventrolateral plates restricted to the actual disk area. SLADEN mentions that "A slight elevation of the surface is present in the median radial line, opposite the base of each ray, and about a third of the distance from the margin to the centre". These radial elevations are very distinctly shown in the published figures, and the present author has not seen any specimens which really do show a similar dorsal aspect. But this appearance cannot be considered of any taxonomical importance; probably the type-specimen of *H. inermis* is with an empty stomach, and with the disk area contracted to such a degree that the skeleton around the closed ambulacral furrows has caused the said dorsal radial elevations.

Distribution:

Hyphalaster inermis is recorded from twenty dredgings in the northern and the tropical part of the Atlantic, from eight dredgings in the Indian Ocean, and from four dredgings in the Pacific. (Fig. 31). It is noteworthy, however, that it has not been taken in any of the rather numerous abyssal dredgings in the eastern Pacific along the American coasts. Its known bathymetrical range is from 2278 to 5413 m (7 finds in less than 3000 m, 11 between 3000 and 4000 m, 9 between 4000 and 5000 m, and 5 in more than 5000 m). It has been found on bottoms of mud, globigerina ooze, and calcareous clay, and at temperatures ranging from 1.1°C. to 3.9°C.

Hyphalaster giganteus Macan, 1938

MACAN 1938 pp. 331-333, pl. $1_{3,7}$.

The description of this species is based on a single specimen dredged by the John Murray Expedition in the Arabian Sea near the Carlsberg ridge (st. 171: about 9°08′N, 53°30′E, 3840-3872 m). It has R/r 82/24 mm; 26 superomarginals, the distal 21 in contact with their opposites; 9 cribriform organs; disk with uniform paxillae with a whorl of 7-9 spinelets surrounding 1-2 central ones. No apical cone. Adambulacralia with 4-5 conical furrow spines and two subambulacral spinelets. Oralia with 7-8 marginal spines and 5 suboral granules. The ventrolateral plates devoid of granules or spines.

MACAN notes that the adambulacral ossicles are mostly badly damaged. It may be inferred, therefore, that the whole ventral side of the specimen is poorly preserved, and that the description of the ventrolateral area as being without spines, perhaps may not have applied to the intact individual. If this is the case, *H. giganteus* is only a large specimen of the species *H. inermis* with which, as also noted by MACAN, it otherwise agrees in all described characters. Specimens of *H. inermis* of a similar large size were also taken by the Galathea in the Indian Ocean. The specific validity of *H. giganteus* at any rate needs confirmation by additional material.

Hyphalaster scotiae Koehler, 1907

KOEHLER 1907 p. 144 (nom. nud.), 1908 pp. 562-565 (226-229), pls. 6_{60}, 7_{71-72}.

This species is described from two specimens with R/r 15.5/8 and 20/10 mm, dredged by the Scotia Expedition in the Atlantic sector of the Antarctic (71°22′S, 16°34′W, 2580 m, blue mud and terrigenous deposits); further was taken a juvenile one with R/r only 6/4.5 mm.

The large specimens have 8 superomarginals, higher than long, joining their opposites from no. 5. Five cribriform organs. A conspicuous terminal ossicle with 4 small spines, viz. a dorsal median one besides the usual 3. Small close-set paxillae with 1 central and 6-7 surrounding spinelets. A small apical cone. Adambulacralia with 3 fairly short conical and pointed furrow spines, and 2 rather similar subambulacral ones. Oralia with about 6 spines marginally, 3-4 smaller spines suborally along the suture, and 2-3 spinelets on the main surface. Ventrolateral plates with conical spinelets.

The juvenile specimen has 3 superomarginals and 3(-4) cribriform organs. A conspicuous terminal ossicle, broad and with a proximal notch, with 5 spines, a large distal terminal one, a pair of smaller subterminal ones, and a granuliform spinelet laterally to each side. A small apical cone. The dorsal side with scattered embryonic plates with 1-2 spinelets, and otherwise covered by large granules. Adambulacralia (in a number of 7) with 4 large and flattened furrow spines (in the arms 3 or 2) and 1-2 subambulacral granules. Oralia with 6 marginal spines and 2-3 suboral granules. Ventrolateral plates with a few granules.

This species is near *H. inermis*, but seems distinguished by having larger subambulacral spines, and further by having relatively fewer superomarginal plates, and more armed terminal ossicles.

Abyssaster gen. nov.

Type-species: *Hyphalaster tara* Wood-Mason & Alcock, 1891.
Syn. *Hyphalaster* Sladen pars.

This new genus is erected to receive three species which were formerly included in the genus *Hyphalaster*, viz. *diadematus* Sladen, 1883, *planus* Sladen, 1883, and *tara* Wood-Mason & Alcock, 1891. Of the two former species only a few specimens are known, whereas several specimens are recorded of the third. This species, therefore, has been chosen as the type of the genus.

Diagnosis:

Porcellanasterids with opposite superomarginals separate to terminal ossicle. All superomarginals unarmed. A mid-interradial suture. Cribriform organs (3-5) confined to disk marginals. Each oral ossicle with a proximal, enlarged mouth-spine.

Description:

The specimens of this group have a subpentagonal disk and fairly broad arms which are only slightly tapering. The ratio R/r ranges from less than 2 in the small specimens to about 2.5 in the largest known, with R about 35 mm. The terminal ossicle is distal to the arm end, fairly conspicuous, and with from 3 to several spines. The inferomarginals of the arms are only slightly lower than their superomarginal companions. In well expanded specimens with full stomachs, the marginals form a perpendicular contour to disk and arms, whereas in contracted specimens with the stomach empty, the superomarginals arch over the dorsal side, so that the opposites in the arms may touch each other above the sunken and wrinkled dorsal integument. The dorsal disk area proper is beset with crowded paxillae, arranged with more or less regular radial (perhaps also interradial) patches of large ones among the main uniform armature of smaller ones. There is an apical appendage, also often in the larger specimens, or at least a distinct apical cone. The integument of the arm bases and the arms is armed with a plating of rounded scales. The jaws show a prominent broad keel formed by the interradial part of the two oralia, which meet proximally and medially, with a fairly broad suture between these places of contact. Each oral ossicle carries a series of up to 7 marginal spines, the proximal one the largest, and possibly some spinelets or granules on its surface. The exposed surface of the primary oral ossicle is in the type-species of a transverse narrow appearance. The adambulacralia are subrhomboid or subcrescentic, with an outward curved furrow margin and 4-7 furrow spines (in the type-species flattened lanceolate). The furrow spines form together a wavy continuous series along either side of the narrow furrow. There is generally no subambulacral armature, though some of the proximal adambulacralia may bear a few granules adorally on their surface. The ventrolateral area is paved with scales, which distally are arranged in radiating rows, corresponding two and two with a marginal plate, and which in the large specimens are armed with spinelets or granules, as is also the surface of the oralia and the adambulacralia. In the arms there is only a narrow strip of naked integument between the adambulacralia and the inferomarginalia.

Key to the species of *Abyssaster*

		Page
1a.	Three cribriform organs. Furrow spines flattened, lanceolate .... *tara*	73
1b.	More than three cribriform organs .... *diadematus* and *planus*	80

Abyssaster tara (Wood-Mason & Alcock, 1891)
Figs. 8-9. Pl. IV.

Hyphalaster tara n. sp., Wood-Mason & Alcock 1891 *b* pp. 434-435, fig. 11.
Hyphalaster tara, Alcock 1893 p. 86.
Hyphalaster tara, Macan 1938 pp. 329-331.

This species was described from a material (number of specimens not stated) obtained by the Investigator in two dredgings in the Bay of Bengal (st. 110: 9°34′N, 85°43′ E, 3650 m, globigerina ooze, 1.7°C.; and st. 117: 11°58′N, 88°52′E, 3200 m, blue mud, 1.8°C.).

The type-specimen has R/r about 18/9 mm, judging from the figure; 6 superomarginals, which are unarmed and according to the description "hardly meet in the middle line along the ray"; 3 papilliform cribriform organs; terminal ossicle fairly large and with 4 spines, a dorsal median one besides the usual 3. Disk with small paxillae with 3-4 spinelets, and five radial bands of larger paxillae with 10-15 spinelets. (The dorsal armature in the arms is not described. The somewhat schematic figure may seem to indicate the presence of paxillae, but erroneously, since the Galathea specimens show a pavement of naked plates). The type-specimens has a well developed apical appendage. Adambulacralia with a fan-like comb of 5-6 compressed lanceolate furrow spines. Oralia with 7 compressed lanceolate marginal spines, of which the proximal one is much enlarged. Ventrolateral plates broad, imbricating ("in ab. nine columns parallel to radial axis"), and with deciduous spinelets.

Macan (1938) records and describes 15 specimens collected by the John Murray Expedition in the Arabian Sea near the Carlsberg ridge (st. 171: about 9°08′N, 53°30′E, 3840-3872 m). The dimensions of seven of these specimens are given as R/r 20/8 to 25/12 mm. Macan notes that "there are 6 superomarginals of which the distal 4 are in contact with their opposites down the length of the ray," (but as will appear from the description of the Galathea material, this applies only to abnormally contracted specimens). There are 18-24 large paxillae in each radial group, arranged in 3 irregular rows. In one of the large specimens, the enlarged paxillae are distributed in more groups in each radius, and further there may be two rows of larger paxillae near the margin of the disk. The adambulacralia bear 5-6 flattened triangular furrow spines. The oralia carry 8-9 marginal spines, and in one specimen there are further 5 suboral granules, whereas the oralia in the other specimens have a naked surface. The ventrolateral plates are stated to be devoid of spines. Eight small specimens have R 6-12 mm, 3-4 superomarginalia, 4-6 furrow spines, and 3 terminal spines only.

The Galathea material:

A total of 62 specimens of *Abyssaster tara* were collected in the Indian Ocean in four different dredgings, off Durban, in the Mozambique Channel, off Kenya, and off Ceylon respectively, viz.

St. 193. 32°34'S, 31°52'E, 3680 m, 1.1°C., globigerina ooze. 3 specimens.
St. 217. 14°20'S, 45°09'E, 3390 m, 1.6°C., globigerina ooze. 3 specimens.
St. 238. 3°23'S, 44°04'E, 3960 m, 1.8°C., globigerina ooze. 33 specimens.
St. 282. 5°32'N, 78°41'E, 4040 m, 1.5°C., blackish mud. 23 specimens.

R/r range in the specimens from st. 193 from 16/7 to 18/9 mm, in those from st. 217 from 13/5 to 20/9 mm, in those from st. 238 from 11/6 to 35/15 mm, and in those from st. 282 from 12/6 to 28/12 mm. The specimens from the two latter stations supplement each other as regards size, 22 of the 23 specimens from st. 282 ranging from R/r 12/6 to 23/10 mm, and 31 of the 33 specimens from st. 238 ranging from R/r 26/11 to 35/15 mm. It therefore seems appropriate to describe the available specimens of these two populations separately.

The population from st. 282, off Ceylon, in the vicinity of the type-locality:

These 23 specimens have R/r as follows: 12/6, 12.5/6, 12.5/6.5, 13/7, 13/7, 14/7, 14/7, 14/8, 15/7, 15/8, 16/8, 17/7, 17/7, 17/8, 18/8, 19/8, 19/9, 19/10, 20/9, 21/9, 22/11, 23/10, and 28/12 mm. The ratio R/r thus ranges from about 1.7 to 2.4. It is $\leqq 2$ in specimens with R up to 16 mm, $\overset{=}{>} 2$ in specimens with R 17-23 mm, and 2.4 in the large one with R 28 mm.

The superomarginal plates (fig. 8*a*, *i*, *s*) are subquadrate or slightly longer than high and show a granulated surface. Their number ranges in these specimens from st. 282 from 4 to 6. Four superomarginals may be found in specimens up to a size of R/r 17/7 mm, but 5 is otherwise the usual number of superomarginals in the medium-sized and also in the smaller specimens available. When only 4 superomarginals are present, also the distal one is well developed and reaches up on the dorsal side of the arm in front of the terminal ossicle. If there are 5 superomarginals, the distal one is situated in its whole length below the terminal ossicle, and still rudimentary and triangular. Also specimens as large as R/r 22/11 mm may have only 5 superomarginals in one or more arms, but the distal one is then always well developed. Six superomarginals is otherwise the usual number in the specimens with R/r 19/9 mm or more, and 6 superomarginals may also be found in specimens with R/r only 15/7 mm.

The inferomarginals are typically situated exactly below their superomarginal partners, in the arms they may however, in some cases be somewhat displaced in relation to these. Towards the end of the arms the inferomarginals become gradually lower than the accompanying superomarginals, so that distally they are only about one-third as high as these. Often there is one additional inferomarginal plate at the tip of the arm.

The cribriform organs number 3 in each arm angle; they are of papilliform structure; and also the papillae of the outer covering series are small.

The terminal ossicle is conspicuous, of a rather obtuse globular appearance, and usually with a faint proximal notch, though also sometimes with the proximal margin simply rounded. It is distal to the arm end, and distinctly larger than this. Typically the terminal ossicle is provided with 4 spines (fig. 8*a*): a distal terminal one, a pair of subterminal ones, and a proximal dorsal and median one. This latter spine may be absent, and the terminal ossicle with only 3 spines, which is the case in a specimen with R/r 14/8 mm, but it may also be substituted by a group of a few spinelets or by a pair of spines, one to either side of the median line, or supplemented by such a pair (fig. 9*a*, *c*). Sometimes there may even be several additional spines on the terminal ossicle, e.g. a spine laterally to either side of the distal terminal one, or two or even three pairs of subterminal spines (fig. 9*e*). The proximal median dorsal spine may be accompanied by a few spinelets adorally, and there may be, as e.g. in the largest specimen, a series of minute spinelets along the lateral ventral margin (fig. 9*h*).

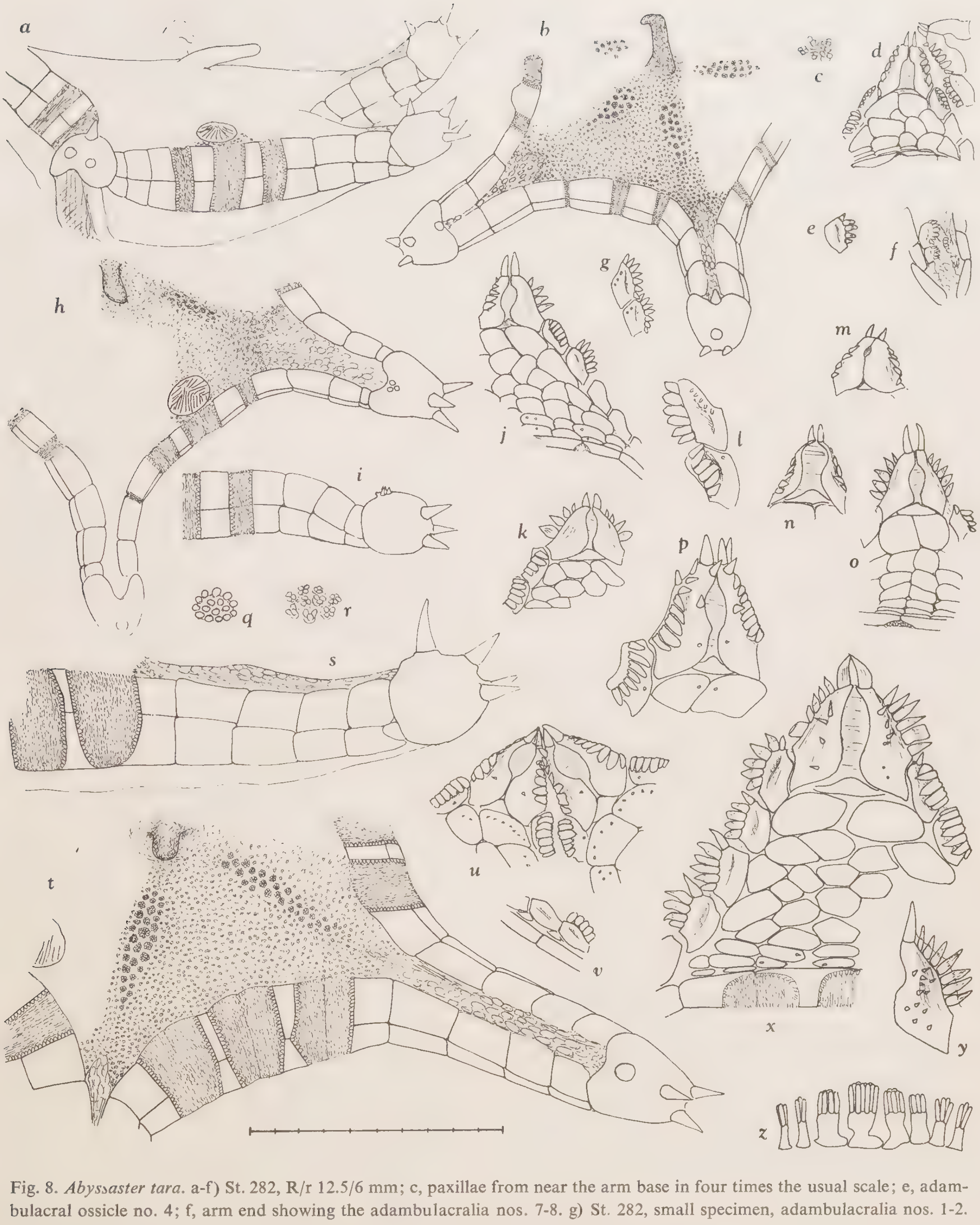


Fig. 8. *Abyssaster tara.* a-f) St. 282, R/r 12.5/6 mm; c, paxillae from near the arm base in four times the usual scale; e, adambulacral ossicle no. 4; f, arm end showing the adambulacralia nos. 7-8. g) St. 282, small specimen, adambulacralia nos. 1-2. h-j) St. 282, R/r 13/7 mm, with four cribriform organs in one interradius; h-i, same arm in dorsal view and in lateral view. k) St. 238, R/r 13/7 mm. l) St. 238, R/r 34/13 mm, adambulacralia nos. 1-2. m) St. 282, r ab. 7 mm. n-o) St. 282, r ab. 9 mm. p) St. 282, R/r 28/12 mm. q-v) St. 282, R/r 23/10 mm; q-r, one of the larger paxillae and a group of the smaller ones in four times the usual scale; s-t, same arm in lateral view and in dorsal view; v, adambulacral ossicle no. 9. x) St. 238, R/r 33/15 mm. y) St. 238, R/r 35/14 mm. z) St. 238, R/r 29/12 mm, paxillae in lateral view, from a tangential line across the disk, showing four enlarged ones and to either side of these the usual smaller ones.

Scale: 10 mm (in c, q, r, and z 2.5 mm).

The central and interradial part of the disk is covered with paxillae, extending as far as to a line connecting the distal end of the second superomarginals, whereas in the arm bases and the arms there is a plating of small rounded plates; the distal ones slightly, or sometimes distinctly larger, and further, more spaced than the proximal ones. The stretch of integument in the arms is in fairly well expanded specimens about half as broad as the terminal ossicle and usually very conspicuous, but in contracted specimens the thin skin of the arms may be sunk and the superomarginal plates almost or actually meeting their opposites above it. This, however, is an artificial state.

The species *tara* has the arms similar to those in SLADEN's *planus* and *diadematus,* which two species it also resembles in other respects. From the type-description of *tara* and from the figure published one might, however, get the impression that *tara* had an armature of paxillae also in the arm bases, and unfortunately MACAN gives no description of the arm armature in his material from the Arabian Sea. Since all other characters agree, it cannot be doubted, however, that the present material represents the species described by WOOD-MASON & ALCOCK.

The paxillae of the main part of the disk are small and generally provided with 3-4 spinelets, this also in the large specimens at hand. The number of spinelets on a paxilla may vary, however, from 2 to 6. Further there are radially arranged groups of larger paxillae, yet hardly discernible in a few of the small specimens (the paxillae in the radial groups here being still only little larger than the others), but already very prominent in other equal-sized small specimens. The patches of enlarged paxillae are more or less distinctly elongate in radial direction, extending a short distance from the center of the disk to usually about the middle of the second superomarginals (fig. 8*t*). In specimens with R/r 13/7 to 14/8 mm the paxillae included in each group number about 7-10 in radial direction and 2-3 across. In the largest specimens the groups of enlarged paxillae likewise number only up to 3 paxillae across, but here there are usually 15 or more paxillae in radial direction. The enlarged paxillae are of diverse sizes within the patches as well as in the different specimens. In a specimen with R/r 23/10 mm the largest paxillae carry up to 16 spinelets.

The paxillar bases form a close pavement in the radial groups of enlarged paxillae, whereas the bases of the other and smaller paxillae of the main part of the disk are spaced. In the present specimens the larger paxillae are often found with their distal part broken off, and then they appear as elongate patches of subhexagonal plates. The smaller paxillae generally have their shafts preserved though they may have lost their spinelets. The reason why the enlarged paxillar shafts are more easily broken than the smaller ones is that they have a marked constriction above the lower part which is attached in the integument. In some of the large specimens, more or less enlarged paxillae are found besides in the radial groups also along the margin of the disk, close to the marginalia or separated from them by a single row of smaller paxillae, and further around the madreporite.

All the specimens at hand have a distinct apical appendage, provided with very minute plates each with one or two minute spinelets.

The madreporic body is subcircular or sometimes transversely oval; in general with the largest diameter about equal to, or a little less than the length of the adjoining marginalia, and with the striae typically radiating from a point quite near the proximal margin. In one specimen, however, it is slightly larger in radial than in tangential direction, and has the striae radiating from an only slightly eccentrical point. The madreporite may lie close to the marginals, or is separated from these by one or sometimes two series of paxillae.

Papulae occur interradially on the disk, but are usually not observable.

The adambulacral ossicles number 10-11 in two specimens with R/r 12.5/6-13/7 mm, 14 in one with R/r 23/10 mm, and 16 in one with R/r 28/12 mm, the number of superomarginals being 5, 6, and 6 respectively. The adambulacralia of the disk area (fig. 8*j, x*) are rather elongate, with an outward curved furrow edge with a comb of generally 5-6 flattened lanceolate and pointed furrow spines which are more or less distinctly curved in abradial direction and have the appearance of segmental papillae at a segmental pit, which extends the whole length of the adambulacral ossicle, and is very distinct on them all, except the distal rudimentary ones below the terminalia. The number of furrow spines occasionally is only 4, as e.g. in a specimen with R/r 17/7 mm, or as many as 7, as e.g. in the two largest specimens, with R/r 23/10 and 28/12 mm. In general there is no subambulacral armature, but some of the most proximal adambulacral ossicles in the larger specimens may adorally on their surface be provided with a single or sometimes 2 or 3 granules.

The oral ossicles of each pair forming a jaw (fig. 8*d, j, m-o, p, u*) are separated by a broad suture and are widely divergent distally where they expose the very broad primary oral ossicle. Each oralia has at its proximal end a large slightly flattened blunt or pointed mouth-spine, and bears along its lateral margin a series of from 3 to 8(-9) smaller spines, the distal ones being larger than the proximal ones. The proximal one to three of these lateral oral spines are often rather spiniform, whereas the more distal ones are distinctly flattened, broad, pointed or blunt, and appear as a series of segmental papillae (see p. 42).

In the small specimens the number of marginal oral spines, inclusive of the large proximal one, is generally 6-7, but may be only 5-6, as e.g. in a specimen with R/r 16/8 mm, or 4-5, as e.g. in a specimen with R/r 17/7 mm. In the large specimens, with R/r 19/9 mm or more, there may be from 6 to 8 oral spines. In the largest specimen available, R/r 28/12 mm (fig. 8*p*), there is even a marginal series of up to 9 spines; and close to the large mouth-spine there may be two additional, slightly smaller spines, below and above it respectively. On the ventral surface of the oralia this specimen may further have a conical spine medially at the suture, and 1-2 granules distally. There may also be a small spine on the inner side of the oral ossicle facing the oral cavity.

The ventrolateral area is covered with a pavement of scales arranged in tangential rows, 6-7 in the small specimens and up to 9-10 in the large ones, and further also in radial series, corresponding two and two with a marginal plate; distally thus in about 8 series, as the ventrolateral plates generally extend to the outer corner of the second inferomarginal plate, or sometimes, when the ventrolateral plates extend as far out as to the proximal part of the third inferomarginals, in 10 series. In the proximal tangential row, at the jaw, the ventrolateral plates number 2, or possibly 3 or 4, and are rather large and irregularly polygonal in shape. The ventrolateral plates in the following tangential rows may also be irregularly shaped, and the radial arrangement in consequence lost. The more distal ventrolateral plates are transversely elongate or subhexagonal in shape, sometimes regularly broadly hexagonal; and usually they are slightly imbricating.

The ventrolateral plates are generally all naked in the small specimens, whereas in specimens with R about 15 mm or more, some of the distal plates usually are provided with a few granules. One specimen with R/r 23/10 mm (fig. 8*u*) has granules also on the proximal plates, in a number of up to about six on the larger ones. In the largest specimen, with R/r 28/12 mm, all the ventrolateral plates appear naked however.

In the arms there is a narrow strip of naked skin between the adambulacral ossicles and the inferomarginals, and the ends of the adambulacral ossicles may be discernible between successive adambulacralia.

The population from st. 238, off Kenya:

These 33 specimens of *Abyssaster tara* have R/r: 11/6, 13/7, 26/11, 27/11, 27/11, 27/12, 29/12, 29/13, 29/13, 30/11, 30/13, 30/13, 30/14, 30/15, 31/13, 31/14, 32/12, 32/12, 32/13, 32/13, 32/13, 32/13, 32/15, 33/13, 33/14, 33/15, 33/15, 34/13, 35/13, 35/14, 35/14, 35/15, and 35/15 mm. The ratio R/r thus ranges from about 2.2 (R 27-33 mm) to 2.7 (R 30-35 mm).

The superomarginals are present in a number of 5 in specimens with R 11-13 mm, 6 in specimens with R 26-27 mm, 7 in specimens with R 29-33 mm, 8 in specimens with R 32-35 mm, and 9 in a few of the largest specimens with R 35 mm. When the number of superomarginals is relatively large in relation to the length of the arms, the distal superomarginal plate is as a rule still rudimentary and situated entirely below the terminal ossicle. The opposite superomarginals remain separate, also in the largest specimens, throughout the whole length of the arms. The inferomarginals as usual are often distally one more in number than the superomarginals.

The cribriform organs are typically present in a number of three in each interradius, the larger organs comprising up to 28-30 rows of papillae. The largest specimens, however, may sometimes be provided with a rudimentary additional cribriform organ to one or to both sides in one or more of the interradii, yet only developed around the suture between the superomarginals. One specimen with R/r 32/15 mm e.g., has 5 cribriform organs in three of the interradii. The 3 median cribriform organs may almost coalesce in the larger specimens.

The terminal ossicles may be even more conspicuous in these large specimens than they were in the above described somewhat smaller specimens from st. 282, although the general rule is that the terminal ossicles become less conspicuous with age. Some of the largest specimens present, with R/r e.g. 33/13 and 35/14 mm, may have the terminal ossicles

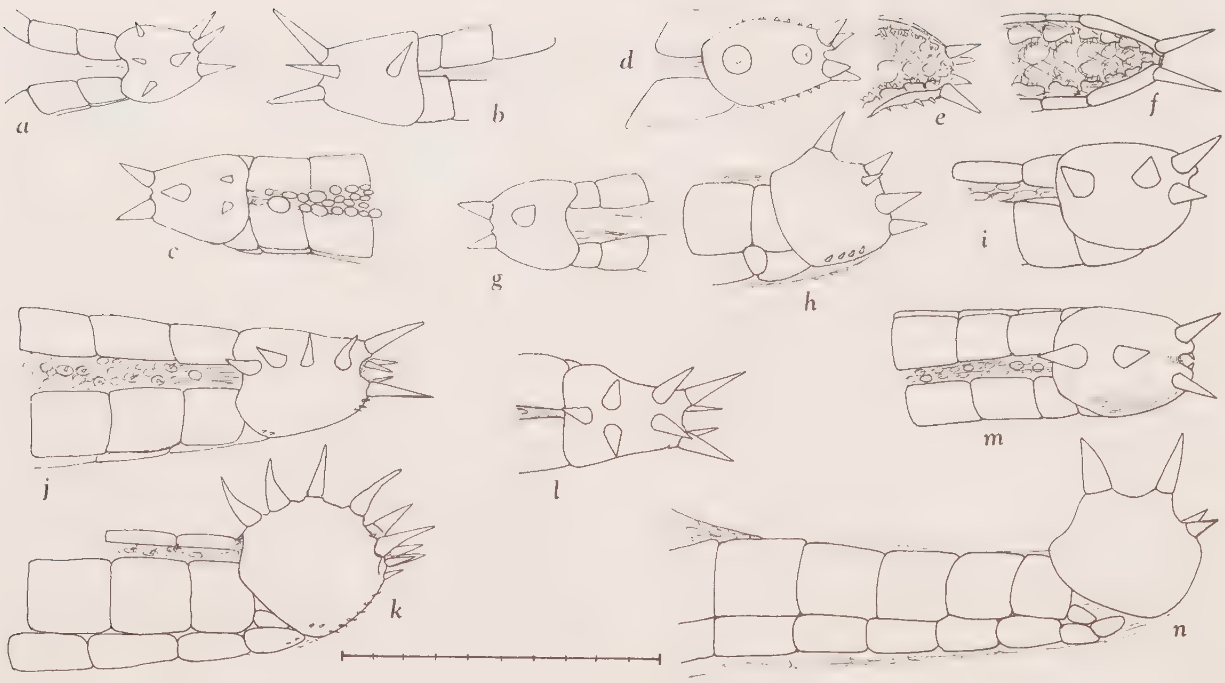


Fig. 9. *Abyssaster tara.* Terminal ossicles; a, st. 282, R/r 16/8 mm; b, st. 193, R/r 18/9 mm; c, st. 282, R/r 19/9 mm; d-e, f, g, h, i, st. 282, R/r 28/12 mm; j-k, st. 238, R/r 32/15 mm; l, st. 238, R/r 30/13 mm; m-n, st. 238, R/r 33/13 mm. Scale: 10 mm.

armed only with the 4 usual spines (fig. 9*m-n*), which are also present in the smallest specimen, with R/r 13/7 mm. Several of the specimens, however, have a much denser armature on the terminal ossicles.

Variations in this armature not met with in the specimens from st. 282 are e.g.: a median row of up to 3 additional spines on the dorsal side of the terminal ossicle, (fig. 9*j-k*); the usual single distal terminal spine replaced by 2 spines in a transverse row, and one or two additional pairs of subequal spines dorsally, or one pair and an unpaired medially placed spine. As in the specimens from st. 282 there may be up to three pairs of subterminal spines (3 spines to each side of the furrow end), and in some few cases the terminal ossicle is furnished with a series of minute spinelets along the ventral margin. The spines on the terminal ossicles may be rather stout, short conical and sometimes with a fairly abrupt tip; but they may also be rather long and slender.

The enlarged paxillae in the radial patches may bear up to 20 spinelets in some of the large specimens from st. 238. But in other specimens the paxillae are less distinctly enlarged. In one specimen with R about 30 mm e.g., the paxillae of the main part of the disk carry (3)4-5 spinelets while the 20-25 enlarged paxillae in the radial patches carry from 6 to 10 spinelets. In the large specimens the radial patches of enlarged paxillae (fig. 8*z*) number 2-3 (rarely 4) paxillae across and from about 6 to 15 in radial direction. In a specimen with R/r 30/14 mm there are e.g. in each radius about 3-4×7 enlarged paxillae with up to 9 spinelets. In another specimen, with R/r 35/14 mm, the patches of enlarged paxillae are 2-3 paxillae broad and reach practically to the arm-bases, the enlarged paxillae carrying from about 6 to 12 spinelets, while those of the main part of the disk carry 3-4(5) spinelets. Some specimens also have 1-3 series of enlarged paxillae along the margin of the disk.

The enlarged paxillae, as it appears from the small specimens with R/r 13/7 mm, initially are developed around 5 radial primary plates which later are absorbed.

In the specimens with R 32 mm or more, some of the dorsal rounded (or subhexagonal) plates in the arms may bear a single spinelet, and those of the arm bases sometimes 2 spinelets. In these large specimens the limit between the paxillae-bearing disk area and the plate-armed arm bases thus may be rather obscured. In the large specimens there are also distally several plates in a transverse direction across the arms, while 1-2 across is the usual in the small specimens.

These specimens from st. 238 have in general a distinct, though short apical appendage, but in some of the large specimens there is only an apical cone, and e.g. in one specimen with R/r 35/15 mm hardly any central prominence is discernible.

Papulae are observed interradially in a few of the specimens.

The adambulacral armature consists of 5-6, occasionally only 4 furrow spines, flattened, more or less curved abradially, typically lanceolate, but the 2-3 median ones often very broad (shovel-like). The proximal adambulacral ossicles carry also sometimes a few granules adorally on their surface.

The oral ossicles (fig. 8*k, x, y*) carry from 5 up to 8 marginal spines and often also a number of suboral granules or spinelets. One specimen with R/r 35/14 mm e.g., has thus about a dozen suboral granules (fig. 8*y*). But specimens as large as R/r 30/13 mm may also have oral ossicles with a naked surface. Sometimes one or more of the distal marginal oral spines are distinctly enlarged. In one specimen with R/r 32/15 mm e.g. the most distal marginal oral spine but one is always very broad and 3-dented.

The ventrolateral plates are arranged in up to 7-9 tangential rows. Those near the margin often bear spiniform granules; and granules may occur also over the greater part of the ventrolateral area, e.g. in a number of about 5 to each of the large proximal plates. Other large specimens, however, apparently may be entirely devoid of ventrolateral spinelets.

The specimens from st. 193 (R/r 16/7, 17/8.5, 18/9 mm) and st. 217 (R/r 13/5, 18/9, 20/8.5 mm) fall mainly within the variation recorded in the materials from sts. 282 and 238. The material from st. 217 shows, however, that 3 terminal spines only may be found also in specimens as large as with R/r 20/9 mm, and further that also specimens of this size may show an additional rudimentary cribriform organ in some interradii.

Remarks:

A diameter of 70 mm (R 35 mm) probably is about as large a size as is attained in the species *Abyssaster tara*, since one of the specimens of that size (R/r 35/14 mm by an empty stomach, 8 superomarginalia and 18 adambulacralia) shows a character which may be interpreted as one of senescence, viz. a tendency of the adambulacral furrow to grow beyond the terminal ossicle.

One of the specimens from st. 238, R 33 mm, was infested with three specimens of *Myzostoma*, attached to the paxillae near the margin.

Yet unripe eggs, 0.35 mm in diameter, filled the gonads of a specimen from st. 238 with R/r 34/16 mm. The gonads open near the middle of the first superomarginal plates, at the outer corner of the cribriform organs.

Distribution:

Abyssaster tara has been dredged in seven localities in the Indian Ocean, scattered along the whole East African coast, and in the region of the Bay of Bengal (fig. 32), at depths from 3200 to 4040 m, on a bottom of globigerina ooze and mud, and at temperatures of 1.1°-1.8° C. The species has further been taken in the North Pacific by the Vitjaz at a depth of 6270-6280 m (BELYAEV in press).

Abyssaster diadematus (Sladen, 1883)

Hyphalaster diadematus n. sp., SLADEN 1883 pp. 237-239; 1889 pp. 159-162, pls. $21_{1\text{-}4}$, $28_{17\text{-}20}$.

This species was described from two specimens dredged by the Challenger off Chile (st. 299: 33°31'S, 74°43'W, 3950 m, blue mud, 1.8° C.).

The type-specimen has R/r 24/10 mm; 10 unarmed superomarginalia, longer than high; 5 cribriform organs. Terminal ossicles with 3 spines. Disk with rather spaced pseudopaxillae with 3-4 spinelets, besides radial irregular groups of about 10 larger paxillae with about 10 spinelets, and interradial groups of a few other large paxillae. An apical cone. Arms from base to terminal ossicle with an integument with small naked plates. Adambulacralia with 4 flattened furrow spines and 5-6 subambulacral granules. Oralia with 6-8 marginal spines, and 6-12 suboral granules. Ventrolateral plates subhexagonal and with 5-6 granules.

The other specimen (that figured on pl. 28) has R/r 14/7.5 mm and 7 superomarginals. Only a small number of enlarged paxillae in rather irregularly arranged groups around the well developed apical appendage; only the most proximal adambulacralia with a few subambulacral granules; and only a few granules on the ventral plates.

A. diadematus seems to be distinguished from *A. tara* primarily by a larger number of marginal plates in relation to size, and by a larger number of cribriform organs.

Abyssaster planus (Sladen, 1883)

Hyphalaster planus n. sp., SLADEN 1883 pp. 242-245, 1889 pp. 165-167, pls. 25_{1-3}, 28_{9-12}.

The single specimen on which this species was based was dredged by the Challenger in the southern Indian Ocean (st. 157: 53°55′S, 108°35′E, 3566 m, diatom ooze, 0° C.).

R/r 35/15 mm; 10-11 unarmed subquadrate superomarginals; 7 cribriform organs; terminal ossicle with 3 spines. Disk with paxillae with 4-6 spinelets (-8 according to figure). Arms from base to terminal ossicle with a dorsal integument with squamiform plates. An apical cone. Adambulacralia with 5-6 flattened furrow spines (4 distally), apparently with a pit on the surface, and with a series of 3-5 subambulacral granules. Oralia with 7 marginal spines and a few suboral granules. Ventrolateral area with oblong squamiform plates, and scattered small granules.

A. planus is likewise distinguished from *A. tara* primarily by a larger number of cribriform organs, and a larger number of superomarginals in relation to size.

Whereas the two forms, *A. diadematus* and *A. planus*, appear to be distinct from *A. tara*, they are, on basis of the descriptions alone, not to be distinguished from each other by any convincing characters, and might well prove to be identical.

Lysaster Bell, 1909

Type-species: *Lysaster lorioli* Bell, 1909.

Diagnosis:

Porcellanasterids with superomarginals forming a complete casing to arms. Superomarginals of disk unarmed, but some in arms with a dorsal spine. A mid-interradial suture. Cribriform organs (7) confined to marginals of disk.

Description:

The disk is pentagonal and the arms are gradually tapering. The cribriform organs are papilliform. The inferomarginals in the arms are only about one-third lower than their superomarginal companions. The terminal ossicle is fairly inconspicuous and dorsal to the arm end. The ratio R/r is a little more than 2 when R about 55-60 mm. The whole dorsal side is closely beset with well-developed paxillae. The furrow spines form a continuous wavy series along the narrow furrow. The ventrolateral plates, and the surface of the oralia and the adambulacralia, are armed with spinelets. The general appearance of the genus is like that of *Hyphalaster* and of *Thoracaster*.

Only 1 species.

Lysaster lorioli Bell, 1909

BELL 1909 p. 21, pl. 3.
FISHER 1919 p. 43.
A. M. CLARK 1952 pp. 945-949, text-figs. 1-3.

BELL in 1909 erected this species and genus for two specimens obtained by STANLEY GARDINER near Mauritius at a depth of at least 500-600 fms. (≧ 1000 m). BELL only gave a short diagnosis accompanied by photos of one of the specimens, and erroneously he registered the form as a pentagonasterid (= goniasterid), not recognizing the cribriform organs, though observing that "the granulation on the margin is so regular that the median suture is often obscured".

FISHER in 1919, after having re-examined the type-specimen, published a more exhaustive description of it. He noted its porcellanasterid habit and considered it a close relative of *Thoracaster*.

Finally A. M. CLARK in 1952 published a detailed description of the two specimens, still the only ones known.

The two specimens have R/r 57/26 and 55/25 mm; 11 superomarginals, joining from plates no. 4 (in the type), and some in arms with a short conical erect dorsal spine; 7 cribriform organs. Terminal ossicle covering two rudimentary superomarginals, and with 3 short spines. Disk with a fairly uniform armature of paxillae with 1-8 central and 8-15 peripheral short spinelets. No apical prominence. Ventrolateral plates probably confined to disk area, and each with about half a dozen short conical spinelets. Adambulacral ossicles rectangular (numbering about 20-21, judging from the photo of the type-specimen), proximal ones with 4 subequal, rather stout pointed furrow spines, and 3 smaller subambulacral spines; distal ones with up to 6 subambulacral spinelets in two irregular longitudinal rows. Oralia with 5-7 marginal spines, that at he tip the largest, and 7-8 suboral spines similar to the distal marginal ones.

Remarks:

A. M. CLARK regards, as also did FISHER, *Lysaster* as most nearly related to *Thoracaster*, which, however, the present author considers at variance with the presence in *Lysaster* of a marginal suture mid-interradially, where in *Thoracaster* there is an odd marginal plate. *Lysaster* rather appears to be related to *Hyphalaster* sensu stricte. (*Thoracaster* and *Hyphalaster*, however, are in most respects very much alike). What primarily distinguishes *Lysaster* from *Hyphalaster* is that its superomarginal spines seem confined to the arms, whereas in *Hyphalaster* they are confined to the superomarginals of the disk, if present at all. *Lysaster* is further distinguished by its smaller number of superomarginals, and by the low ratio of R/r, only little more than 2 in large specimens.

Benthogenia Fisher, 1911

Type-species: *Benthogenia cribellosa*, Fisher 1911.

Diagnosis:

Porcellanasterids with arms encased by superomarginals, each with a dorsal spine, while those of arm angle are unarmed. A mid-interradial suture. Cribriform organs around all vertical marginal sutures, clear to terminal ossicle.

Description:

The disk is subpentagonal with the gradually tapering arms springing from a fairly wide base, the first joining opposite superomarginals being much larger than those bounding the disk. The inferomarginals of the arms are distinctly lower than their superomarginal companions. The cribriform organs are papilliform. The terminal ossicle is dorsal to the arm end, and provided with several spines. R when 78 mm, is about $2^1/_2$ r. The whole dorsal side is armed with close-set well-developed paxillae. The adambulacral spines form a continuous wavy series along the narrow furrow. The jaws are prominent, with a wide suture; and each oral ossicle carries a series of marginal spines. The whole ventral surface inclusive that of the oralia and the adambulacralia, is closely armed with spinelets. The general appearance of the genus is rather like that of *Hyphalaster*, and of *Thoracaster*.

Only 1 species.

Benthogenia cribellosa Fisher, 1911

Fisher 1911 *a* pp. 415-417.
Fisher 1919 pp. 39-4 3, pls. 1_1, 2_1, 8_2.

This species and genus was described from a single specimen collected by the Albatross in the Philippine region (st. 5513: 8°17′N, 124°03′E, 925 m, gray mud and fine sand, 11.5° C.). Fisher in 1919 gave a more thorough description of the same specimen, and also published some figures, and further he recorded three juvenile specimens of the genus from another dredging in the region (Albatross st. 5425: near Cagayanes Island, Sulu Sea, 905 m, gray mud and coral sand, 9.7° C.).

The type-specimen has R/r 78/30 mm; 17 superomarginals, contiguous along midline of arm from plates no. 6, higher than long, and those of first joining pair much the largest. Each superomarginal plate in arms with a short conical dorsal spine. Cribriform organs around every vertical marginal suture, and also extending up on dorsal surface of arms. Terminal ossicle entirely dorsal to arm end, elliptical and with up to 7 spines, viz. a row of 3 in the median dorsal line and 2 to either side distally. Paxillae with 5-15 central and 15-20 peripheral spinelets. Papulae numerous. No apical appendage. Adambulacral ossicles subrectangular, with 7-8 compressed furrow spines, and 10-12 subambulacral spinelets in about two longitudinal series. Number of adambulacralia probably not much larger than that of marginalia. Oral ossicles with 12 marginal spines, the proximal lanceolate one much the largest, and about 15 suboral spinelets in two irregular series. Ventrolateral plates extending nearly to end of arms, those of disk area slightly imbricating and with 5-12 spinelets.

The juvenile specimens range from R 5.5 mm and 4 superomarginals to R 12 mm and 10 superomarginals. In the large one the superomarginals join from the sixth opposite pairs, and one or two in arms bear a dorsal spine. Terminal ossicle with 4 spines, and only with its distal half overlying the superomarginals. Cribriform organs at every marginal suture, but those of arms yet rudimentary. Dorsal paxillae with only 4-5 spinelets. A prominent apical peduncle. Adambulacralia with 5 furrow spines and 0-2 subambulacral spinelets. Oralia with 8 marginal spines and a few suboral spinelets. Fisher notes that he is not quite sure that the juvenile specimens of *Benthogenia* really belong to the species *cribellosa*, which, however, there seems no reason to doubt.

According to Fisher, *Benthogenia* probably is nearest *Hyphalaster*. And that it is closely related to this genus cannot be questioned, but its nearest relative among the other porcellanasterid genera, however, seems to be *Lysaster*. *Benthogenia* and *Lysaster* both have a low number of superomarginals, and both possess superomarginal arm spines, and appear to differ primarily by the cribriform organs being developed around all the vertical sutures in the former, but in the latter only around the interbrachial ones. In *Benthogenia* the inferomarginals also are comparatively much lower than in *Lysaster*.

Thoracaster Sladen, 1883

Type-species: *Thoracaster cylindratus* Sladen, 1883.

Syn.: *Pseudaster* E. Perrier, 1885 (type-species: *Pseudaster cordifer* Perrier, 1885 = juv. *Thoracaster cylindratus* Sladen).

Diagnosis:

Porcellanasterids with superomarginals forming a complete casing to arms, devoid of larger spines, but possibly covered with minute spinelets. An unpaired superomarginal and accompanying inferomarginal plate in the interradial midline. Cribriform organs generally confined to marginals of disk.

Description:

The disk is subpentagonal with the arms well set off, cylindroid and gradually tapering. The cribriform organs are papilliform. The inferomarginals of the arms are about two-thirds to half as high as their superomarginal companions. The terminal ossicle is fairly inconspicuous and rather distal to the arm end. The ratio R/r ranges from about 2 in small specimens to almost 4 in some of the large ones with R about 100 mm. The shape is rather flat even when the stomach is well filled. The whole dorsal side is armed with crowded well-developed paxillae. The adambulacralia are subrhomboid or subrectangular, with the furrow margin only slightly curved, and with a series of furrow spines connected by a basal web and together forming a continuous almost straight series along the narrow furrow. The jaws are moderately prominent. The oralia meet proximally, and medially, and each carries a series of marginal spines, the proximal one of which is somewhat enlarged. The ventrolateral area is paved with fairly small imbricating plates, and small ventrolateral plates extend down the arms. The whole ventral side, including surface of oralia, primary oral ossicle and adambulacralia, is covered with spinelets. The marginalia may be almost uniformly covered with minute spinelets.

Only 1 species.

Remarks:

Sladen erected *Thoracaster* for his species *cylindratus*, and two other species have later been described, viz. *T. magnus* by Ludwig in 1907, and *T. alberti* by Koehler in 1909. The form *Pseudaster cordifer* of E. Perrier 1885 has proved to be based on a juvenile *Thoracaster cylindratus*, and also the specimen listed by Chun in 1900 as *Hyphalaster valdiviae* n. sp. (on the basis of Ludwig's preliminary identification), and the specimen mentioned by Richard in 1903 as *Hyphalaster* n. sp., have been found to belong to *Thoracaster cylindratus*.

Thoracaster resembles *Benthogenia, Lysaster,* and *Hyphalaster* in general appearance, but is, among other things, characterized by having an odd superomarginal and accompanying inferomarginal plate in the interradial midline instead of a suture as in all the other porcellanasterid genera hitherto described.

(Another genus, *Vitjazaster,* from the western North Pacific, which will be described by Belyaev, agrees with *Thoracaster* in having an odd marginal plate in the interradial midline, but is well distinguished by other characters, e. g. by the appearance of the ventrolateral armature and by having the arms provided with an armature of dorsal plates).

The genus *Thoracaster* has hitherto been recorded from 12 localities, in the tropical Atlantic, in the Indian Ocean, and in the eastern Pacific respectively, in a total of 26 specimens. The Galathea Expedition brought back 37 specimens from seven dredgings in the Indian Ocean, and the infraspecific variation found in this large material has convinced the present author that all recorded specimens of *Thoracaster* belong to one and the same species.

Thoracaster cylindratus Sladen, 1883
Figs. 10-11. Pls. V-VI.

Thoracaster cylindratus n. sp., Sladen 1883 pp. 245-247; 1889 pp. 168-170, pl. 29_{1-6}.

Pseudaster cordifer n. sp., E. Perrier 1885 *a* p. 286 (nom. nud.); 1885 *b* pp. 67-69; 1894 pp. 235-237, pl. 16_{3-3e}.

Hyphalaster valdiviae n. sp., Ludwig, in Chun 1900 p. 490.

Thoracaster magnus n. sp., Ludwig 1907 pp. 313-314.

Thoracaster alberti n. sp., Koehler 1909 *a* pp. 45-48, pls. 3_{1-4}, 5_7.

Thoracaster cylindratus, Koehler 1909 *b* pp. 41-41, pl. 18_1.

Thoracaster magnus, H. L. CLARK 1920 pp. 78-79, pl. 1_{1-2}.
Thoracaster cylindratus, LIEBERKIND 1932 pp. 285-288, texfig. 10, pls. 2_{1-2}, 3_{12-14}, 4_{1}, 6_{5-8}.
Thoracaster magnus, FISHER 1928 p. 487.
Thoracaster cylindratus, MADSEN 1951 p. 83.

T. cylindratus was described by SLADEN from a single specimen dredged by the Challenger in the eastern Atlantic near the Cape Verde Islands (st. 89: 22°18′N, 22°02′W, 4390 m, globigerina ooze, 2.6°C.). It has R/r 62/21 mm; 21-22 unarmed superomarginals to each side of the unpaired interbrachial one, slightly higher than long, and, judging from the figures, joining from nos. 7-8 (not counting the unpaired plate); 14 cribriform organs. Terminal ossicle inconspicuous, naked. Dorsal area with closely crowded small paxillae with 6-10 spinelets. Adambulacralia with 5 subequal furrow spines, and two irregular rows of about 3 and 5 subambulacral spinelets. Oralia with 6-7 subequal marginal spines and a larger number of suboral spinelets. Ventrolateral plates with a close covering of minute subspiniform granules. (The description of the furrow spines as short and flat apparently only refers to their distal part, protruding outside the thick basal web connecting them).

Pseudaster cordifer: E. PERRIER (1885, 1894) described this form from a single specimen collected by the Talisman near the Azores (st. 134: 42°19′N, 23°36′W, 4060 m, soft, white mud). It has R/r 9/6 mm; 4 superomarginals to either side of an unpaired interradial one; 5-6 inferomarginals; 8 rudimentary cribriform organs. Terminal ossicle broad, with a proximal notch and 3 small spines. Dorsal area with "a regular granulation". A small apical appendage. Adambulacralia rectangular, with 4-5 furrow spines and 3-4 subambulacral spinelets. Oralia with 7 marginal spines, 3-4 suboral spinelets along the suture and 3 distally. Ventrolateral plates with a few minute spinelets.

PERRIER in 1894 in a foot-note says that the presence of an unpaired interradial marginal plate was very remarkable for a porcellanasterid, and might perhaps be an individual anomaly in the described specimen. He had thus overlooked that SLADEN already had described this feature from *Thoracaster cylindratus.*

LUDWIG (1907 p. 313) stated that *Pseudaster cordifer* was a juvenile *Thoracaster cylindratus,* – on basis of his knowledge of the variation with age in *Thoracaster* from his own material from the Pacific, including specimens ranging from R 20 to 98 mm (cf. below). (Juvenile specimens of *Thoracaster* agreeing with the description of *Pseudaster cordifer* are also present in the Galathea material).

A specimen of *Thoracaster* was collected by the Valdivia Expedition in a dredging off Liberia (st. 45: 2°56′N, 11°40′W, 4990 m, yellow-brown mud, 2.4°C.) not far away from the type-locality of *T. cylindratus.* Ludwig preliminarily considered it as representing a new species of *Hyphalaster,* for which reason it was listed under the name of *Hyphalaster valdiviae* (a nom. nud.) by CHUN in 1900. In 1907 p. 313 LUDWIG, however, stated that the specimen in question in fact belongs to the species *Thoracaster cylindratus.* A detailed description of it was finally given by LIEBERKIND in 1932. It has R/r 67/21 mm; 22 superomarginals to each side of the unpaired median one; 13 fully developed cribriform organs and a few rudimentary ones; naked terminalia. It shows a slight variation from the type-specimen by having minute plates inserted here and there between the otherwise joining superomarginals proximally in the arms.

Thoracaster cylindratus was further recorded by KOEHLER (1909*b*) from two Princesse Alice dredgings near the Azores (st. 753: about 39°50′N, 18°W, 4360 m, globigerina ooze, and st. 1306: about 37°17′N, 20°13′W, 4275 m, globigerina ooze), 3 and 1 specimen respectively. The latter specimen was preliminarily listed by RICHARD (1903 p. 66) as *Hyphalaster* n. sp., and the station by a lapse given as st. 1036. The three specimens from st. 753 had R/r 75/22, 76/22, and 80/23 mm; 25/26 superomarginals to each side of the unpaired one, and 14 cribriform organs. The specimen from st. 1306 is a juvenile with R/r 12/7 mm, 7 superomarginals to each side of the unpaired one, 6 cribriform organs, terminal ossicle with 3 spines. It corresponds, as KOEHLER notes, in general appearance to the specimen described by PERRIER as *Pseudaster cordifer.*

Two specimens of *Thoracaster cylindratus* were recorded by the present author (1951) from a dredging of the Swedish Deep-Sea Expedition in the western tropical Atlantic (st. 342: about 2°25′N, 39°19′W, 4474-4430 m, calcareous clay, 1.3°C.). They have R/r about 43/14 and 46/16 mm, 18 and 20 superomarginals besides the unpaired one, and 12-13 and 13-14 cribriform organs.

Thoracaster magnus: This form was described by LUDWIG in 1907 on the basis of 9 specimens collected by the Albatross in four dredgings in the tropical eastern Pacific off Peru (st. 4647: 4°33′S, 87°43′W, 3667 m, globigerina ooze, 1.9°C.; st. 4649: 5°17′S, 85°20′W, 4088 m, grey mud, 1.9°C.; st. 4658: 8°30′S, 85°36′W, 4335 m, green mud, 1.8°C.; and st. 4717: 5°11′S, 98°56′W, 3938 m, globigerina ooze, 1.8°C.). The same material was described and figured by H. L. CLARK in 1920. R/r range from 23/? to 98/32 mm. Specimens with R 72-98 mm have 22-24 superomarginals besides the unpaired one, and 14 cribriform organs. Terminal ossicles inconspicuous and with a pair of small spines ventrally. Dorsal paxillae with up to 30 spinelets. Small plates proximally in the dorsal midline of the arms, between the opposite superomarginals. Papulae interradially. Ambulacralia with 4-5 furrow spines and 3-4 smaller subambulacral spines. Oralia with 8 marginal spines and 10-12 smaller suboral ones. Ventrolateral plates, according to LUDWIG, with a more robust, but sparser spine-armature than in *T. cylindratus*.

LUDWIG states as the character primarily distinguishing *T. magnus* from *T. cylindratus* that the superomarginal plates of both sides of the arms only join immediately in the distal part, whereas in the proximal part they are separated by a series of minute plates. As other distinguishing features LUDWIG mentions the larger number of paxillar spinelets, the broader cribriform organs, and the more robust ventrolateral spine armature. All these differences, however, are accounted for by the larger size of several of the specimens of *T. magnus*.

H. L. CLARK in 1920 p. 79, gave a more detailed description of the appearance of the dorsal arm plates and their distribution in *Thoracaster magnus*. He writes e. g.: "In a specimen with R = 23 mm. this series (i. e. of abactinal plates which extends to the tip of the arm or nearly so) is .60 mm wide clear to the terminal plate; ... In a large specimen, with R = 73 mm., the plates do not reach the extreme tip of the arm, but are shut off from the terminal plate by the meeting of three pairs of superomarginals; ...".

LIEBERKIND, as mentioned above, found some minute plates inserted between the opposite superomarginals proximally in the arms of the Valdivia specimen of *T. cylindratus*, for which reason he began to doubt the specific validity of *T. magnus*. He re-examined one of the original specimens of this form and found only some unimportant differences from the type of *T. cylindratus*, e. g. in the appearances of the spinelets of the dorsal paxillae and of the cribriform organs. LIEBERKIND noted also that he was inclined to believe that a larger material would show intermediate characters, the two forms in question in reality being only two geographical races of the same species; but, nevertheless, he considered it the most appropriate provisionally to retain them as separate species.

Incidentally, LIEBERKIND makes a lapse in his discussion of the forms of *Thoracaster* described. He refers, p. 287, to H. L. CLARK's statement, op. cit. p. 79, that "In another particular, *magnus* differs markedly from the other two species of the genus (*cylindratus* and *alberti*), and that is in the series of abactinal plates which extends to the tip of the arms ...". And then he claims that CLARK is not right in considering this a difference from *T. cylindratus* since, he says, the figures SLADEN gives, distinctly show the same feature although SLADEN does not mention it in his text. This remark, however, is only understandable if it is assumed that LIEBERKIND has misread "abactinal" in CLARK's text as "actinal", since what he had in mind can only have been the series of ventrolateral plates extending down the arms.

A single, large specimen of *Thoracaster*, collected by the Arcturus in the tropical eastern Pacific (st. 53: 1°51′S, 89°50′W, 3170 m), was recorded by FISHER in 1928 as a *T. magnus*.

The differences between *T. cylindratus* and *T. magnus* stated in the literature appear quite unimportant taxonomically, and when dealing with *Thoracaster cylindratus* in 1951, the present author, therefore, listed *magnus* as a synonym, a view which the study of the specimens collected by the Galathea confirms.

Thoracaster alberti: KOEHLER (1909*a*) described this species from 7 specimens dredged by the Investigator in the Arabian Sea (st. 287: 21°09′N, 65°47′E, 2755 m, green clay, 2.8°C.). R/r 45/17 mm in one specimen, about 60/20 to 60/21 mm in the others; 17-18 superomarginals besides the unpaired one, joining from nos. 5-6 (exceptionally no. 7), subquadrate interbrachially, rectangular in arms; 14 cribriform organs. Median part of the marginals of the disk provided with small pointed spines in 1-3 irregular vertical rows between the cribriform organs; also the proximal arm marginals with an armature of spinelets. Terminal ossicle inconspicuous, with 3 small spines. Dorsal paxillae with 20-30 granules. Sometimes a faint apical cone. Adambulacralia with

4 flattened subequal furrow spines, and 3-4 granuliform subambulacral spinelets. Oralia with about 10 marginal spines (7-8 are shown in the figure 7, pl. 5), and a larger number of suboral ones. Ventrolateral area uniformly covered with spiniform granules.

Thoracaster alberti should be distinguished from *T. cylindratus* by the armature of spinelets between the cribriform organs; but this is a character of uncertain taxonomical value. H. L. CLARK recorded spinelets dorsally and ventrally on the marginals between the cribriform organs also in the material of *T. magnus*. And the present material of *Thoracaster* from the Galathea Expedition has shown that the spine-armature of the marginals is really very variable. The conclusion therefore is that also *T. alberti* is the same species as *T. cylindratus*.

The Galathea material:

A total of 37 specimens of *Thoracaster* was collected in seven dredgings in the Indian Ocean, viz. two off East Africa north of Madagascar, three near Ceylon, and two in the Bay of Bengal.

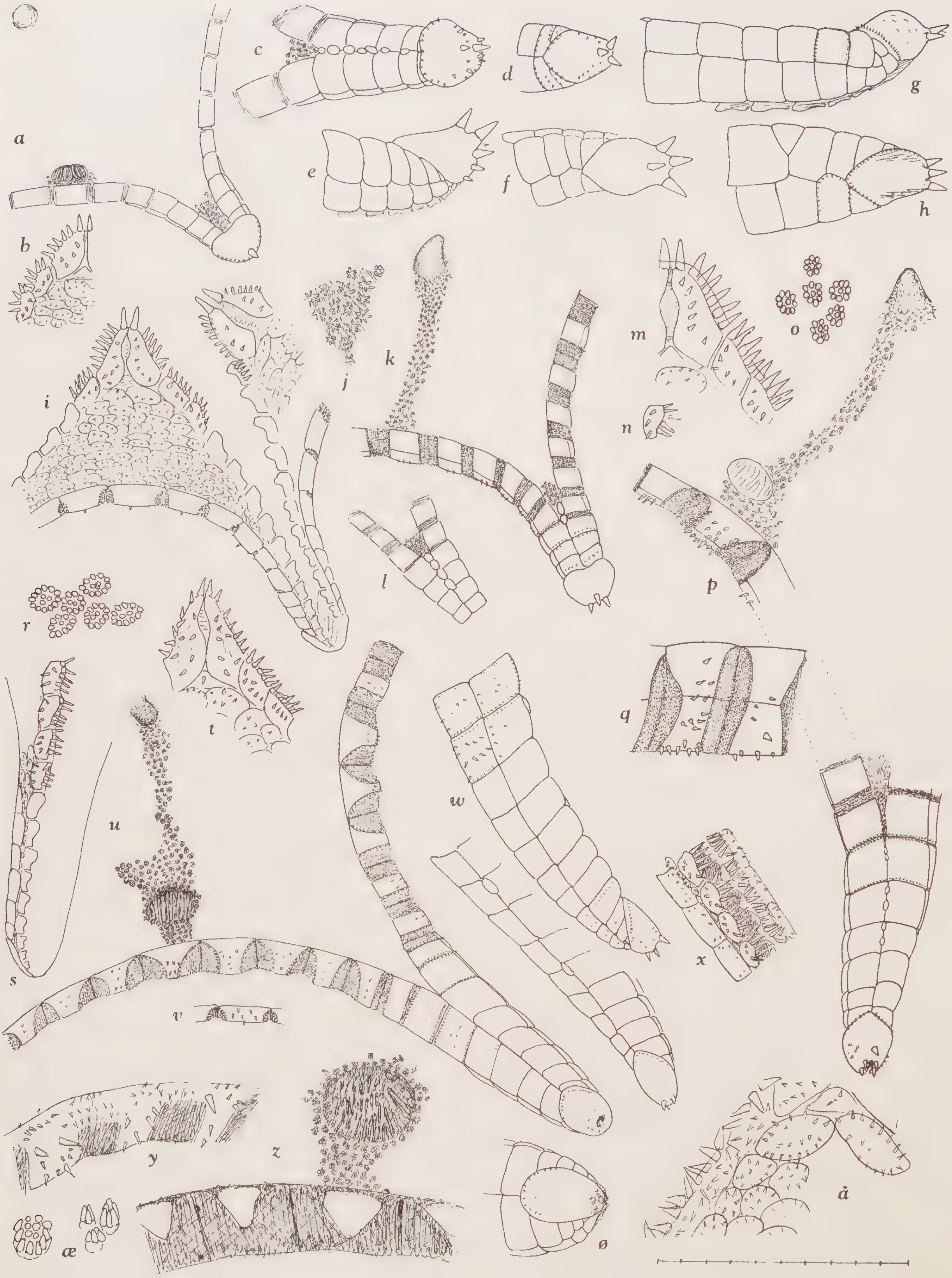
St. 232: 9°03′S, 49°22′E, 4930 m, 1.3°C. 1 specimen.
St. 238: 3°23′S, 44°04′E, 3960 m, 1.8°C., globigerina ooze. 3 specimens.
St. 280: 1°56′N, 77°05′E, 4350 m, 1.3°C., globigerina ooze. 2 specimens.
St. 281: 3°38′N, 78°15′E, 3310 m, 1.8°C., globigerina ooze. 6 specimens.
St. 282: 5°32′N, 78°41′E, 4040 m, ca. 1.5°C., blackish mud. 1 specimen.
St. 299: 17°10′N, 84°30′E, 2820 m, 1.7°C., mud. 1 specimen.
St. 314: 15°54′N, 90°17′E, 2600 m, 1.7°C., brownish ooze. 23 specimens.

The single specimen from st. 232 (pl. VI 7) has R/r 101/30 mm; about 28 superomarginals (not counting the unpaired one), and 22 cribriform organs. The three specimens from st. 238 have R/r 89/28, 100/27, and 103/30 mm, 24, 23 and 24 superomarginals respectively, and 13-14, 11-14 and 12-13 cribriform organs. The two specimens from st. 280 have R/r 84/22 and 86/24 mm, 24 and 25-26 superomarginals, and 14 cribriform organs. The six specimens from st. 281 have R/r 13/7, 20/10, 41/12, 42/12, 64/20, 66/23 mm, and 7, 10, 18, 18, 24, and 21 superomarginals respectively, the two small specimens 4-6 and 8-10, the medium-sized ones 12-14, and the two larger ones 14 and 12 cribriform organs. The single specimen from st. 282 has R/r 87/23 mm, 24-26 superomarginals, and 14-16 cribriform organs. The single specimen from st. 299 has R/r 31/11 mm, 14 superomarginals, and 14 cribriform organs. The material of 23 specimens from st. 314 includes ten juveniles with R/r ranging from 14/6.5 and 14/7 mm to about 24/9 mm, 8 to 10 (11 ?) superomarginals, and 10 to 12 cribriform organs. Another small specimen has R/r 26/11 mm, 13 superomarginals, and 12 cribriform organs. Five larger specimens have R/r 54/21, 55/19, 60/21, 61/21, and 70/21 mm, 17, 19, 19, 22, and 22 superomarginals, and 12-13, 12, 16, 14-15, and 14 cribriform organs respectively. The remaining seven specimens from st. 314 are also medium-sized ones with R about 60-70 mm, but very damaged.

The material of *Thoracaster* thus comprises both juvenile specimens (corresponding to PERRIER's *Pseudaster cordifer*) as well as specimens as large as or slightly larger than any hitherto on record. Specimens with R/r about 25/10 mm or more, show full-grown characters, and the largest specimens available show in part what must be considered senescent characters. The ratio R/r is hardly 2 in the smallest specimens, about 2.5 in the smaller ones with the full-grown characters, increases to about 3 in the medium-sized specimens with R 50-60 mm, and to almost 4 in a few of the largest specimens present.

The description of the specimen from st. 282 with R/r 87/23 mm (pl. V) is used as a starting point in the following survey of the present material and of its variation.

The superomarginals in the specimen with R/r 87/23 mm number 24-26 to each side of the mid-interradial unpaired plate, and join their opposites in the mid-dorsal line from about no. 7, the unpaired plate not included. In most of the other full-grown specimens, however, the superomarginals join from the eight opposite pair. In a few specimens they do not join until the ninth plates, and one of the largest specimens, with R/r 101/30 mm and 28 superomarginals, is distinguished by having these separate as far as to the tenth or eleventh opposite pairs. (This specimen has also unusually many cribriform organs). A juvenile specimen with R/r 13/7 mm has all the 6-7 paired superomarginal plates separate (fig. 10*a*). Another juvenile with R/r 14.5/7 mm has 8 superomarginals which join from no. 6 (fig. 10*k*). The superomarginals of either side of the arms are usually exactly opposite each other (fig. 10*p*), but may in rare cases subalternate (fig. 11*a*). The distal 2-3 superomarginals are rudimentary and situated below the terminal ossicle.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The marginals bordering the disk are all subquadrate. In the arms the superomarginals are higher than long, distally up to twice as high as long.

The inferomarginals are proximally in the arms only slightly lower than their superomarginal companions, but decrease towards the arm end relatively more in height. Below the terminal ossicle there is often 1-2 inferomarginals more than superomarginals. The inferomarginal plates in general are arranged exactly corresponding with the superomarginal ones, but in some specimens they may subalternate with these for a varying length of the arms. LIEBERKIND (1932 p. 285) described a subalternation of the marginals in the Valdivia specimen, and noted that "Inwieweit es sich hier nur um eine individuelle Variation handelt, kann ich nicht mit Sicherheit bestimmen, da ja nur ein Exemplar vorliegt". In this connection it may be emphasized that the typical regular arrangement of the marginal plates has been found subject to individual variation in almost every population of porcellanasterids studied here, and especially, of course, in the long-armed forms.

The inferomarginals of the disk in the specimen with R/r 87/23 mm bear ventrally two small spines (distinctly larger than the ventrolateral spinelets) placed with one to each lower corner of the cribriform organs; and the proximal inferomarginals of the arms have a single similar small spine placed medially near the margin. All the marginal plates are further provided with a series of close-set minute spinelets along their margins (fig. 10*h*).

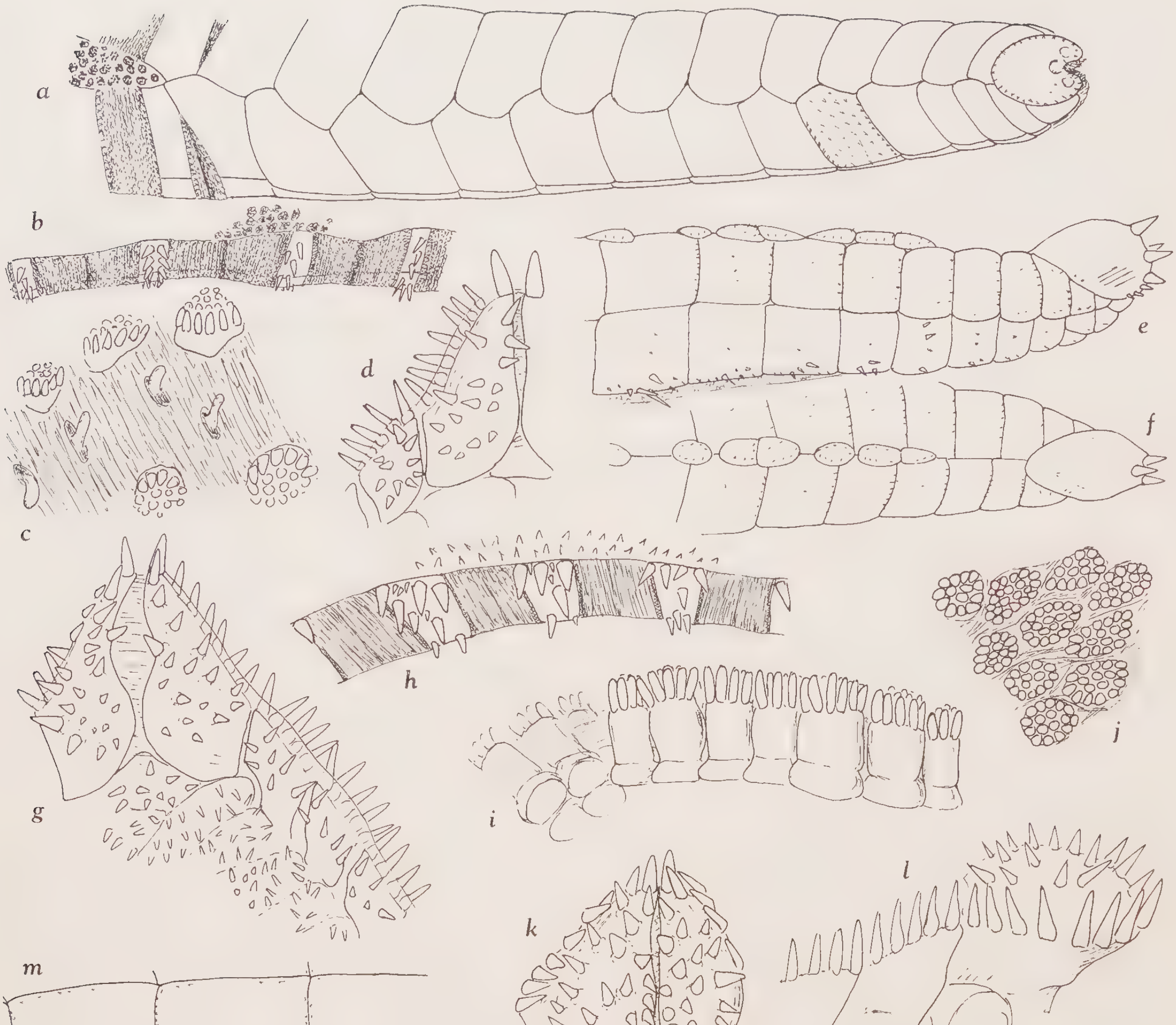
Some other specimens show an even more developed spine-armature on the marginals. Between the cribriform organs there may be one or two medial irregular rows of some small spines, and at the lower edge of the inferomarginals 3-4 small spines besides some spinelets, e. g. in the specimens from sts. 314 and 238, with R/r 54/21 and 89/28 mm respectively, as shown in fig. 11*b* and *h*. Minute spinelets may also be scattered over the surface of all the marginals, and sometimes even form a uniformly spaced covering (fig. 11*a*). The series of minute spinelets along the vertical sutures may appear rather like the fascioles in the astropectinids, or as rudimentary cribriform organs (figs. 10*w*, 11*n*).

The character which should distinguish KOEHLER's *T. alberti* from SLADEN's *T. cylindratus* was, as noted, an armature of minute spines between the cribriform organs. The most spiny specimens of the present material represent the form *T. alberti*, whereas a specimen as that with R/r 87/23 mm, with regard to the spine-armature represents a condition transitional to that of the type of *T. cylindratus*, with no spine-armature between the cribriform organs (to which condition there is but a slight step). The rather small specimens of *Thoracaster* collected by the Swedish Deep-Sea Expedition in the Atlantic had a few small spines along the ventral edge of the inferomarginals, the two at each side of the cribriform organs being the larger. Also specimens of LUDWIG's *T. magnus*, according to H. L. CLARK, have minute spines or spinelets at the ventral and dorsal margins of the marginal plates between the cribriform organs. (Such spinelets further may be easily rubbed off and lost). The conclusion can only be that it is impossible to upheld *T. alberti* as a distinct species.

Cribriform organs occur in the specimen with R/r 87/23 mm in a number of 14 fully developed ones in each interradius, and there may further be an additional rudimentary organ to either side of this series, and in some interradii thus up to 16 cribriform organs in all. The cribriform organs are of a papilliform structure. Each organ in the specimen with R/r 87/23 mm may comprise as many as 30 rows of papillae, and the median organs may join their neighbours at the dorsal edge of the superomarginals and almost meet also at the horizontal suture, whereas they narrow somewhat down towards the ventral edge of the inferomarginals.

A varying number of the median cribriform organs in the large specimens usually coalesce with their adjacent partners at the horizontal suture, leaving free only a ventral triangular area on the inferomarginals, with a few small spines, and a similar

Fig. 10. *Thoracaster cylindratus*. a-b) St. 281, R/r 13/7 mm. c) St. 281, R/r 20/10 mm. d) St. 281, R/r 41/12 mm. e-f) St. 280, R/r 86/24 mm, two different arms. g-h) St. 282, R/r 87/23 mm, arm in lateral view and in dorsal view respectively. i-k) St. 314 R/r 15/7 mm; j, paxillae in four times the usual scale. l) St. 314, small specimen, base of arm in dorsal view. m-q) St. 299, R/r 31/11 mm; n, adambulacral ossicle no. 10; o, paxillae in four times the usual scale; q, odd marginals and first paired marginals (to the right). r-v) St. 314, R/r 26/11 mm; r, dorsal paxillae in four times the usual scale; v, paired inferomarginal plate no 1 in ventral view. w-x) St. 314, medium-sized specimen; w, arm in dorsal view and in lateral view, spine-armature indicated on some of the marginals; x, ventral view of same arm. y-å) St. 314, R/r 55/19 mm; y, odd inferomarginal plate and paired inferomarginals nos. 1-2 (to the right) in ventral view; z, part of disk with madreporite; æ, large and smaller paxillae in four times the usual scale; å, part of ventral side with the adambulacralia nos. 1-3.
Scale: 10 mm (in j, o, r, and æ 2.5 mm).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triangular area dorsally on the superomarginals, or, if also coalesced dorsally, only a small patch centrally on each superomarginal plate. The rudimentary cribriform organs may be developed from the dorsal and the ventral edge of the marginals simultaneously.

The number of cribriform organs in a juvenile specimen with R/r 13/7 mm is still only 4-6 in each interradius, but others of about similar size have already 8-10 (12) such organs. All the specimens at hand with R/r about 25/10 mm or more, have at least 12 cribriform organs developed. The largest known specimens, with e. g. R/r 103/30 mm, may also have only 12 cribriform organs, but 14 to each interradius is most common, and is found also in specimens as small as with R/r 31/11 mm. Besides the specimen with R/r 87/23 mm, only a single other one, with R/r 60/21 mm, has 16 cribriform organs.

The extraordinarily high number of 24 cribriform organs in each interradius, is found in the specimen with R/r 101/30 mm, one of the largest available and that with the largest disk, i. e. largest number of interbrachial marginals, its superomarginals not meeting in the arms until nos. 10-11. (Pl. VI 7). The series of cribriform organs in this specimen consists of 18 fully developed organs (with up to about 30 rows of papillae) and to either side of these 2 rudimentary ones. Sixteen of the organs are coalesced at the horizontal suture, and the median ones also ventrally and dorsally, so that the marginals have only a small central patch free. The rudimentary outermost organs reach from the ventral margin of the inferomarginals half-way up on the superomarginals, or only to the horizontal suture.

In the specimen with R/r 87/23 mm, a varying number of small rounded plates is found in the midline of the arms, inserted between the two rows of otherwise joining superomarginals. They occur in a continuous series for a distance of eight pairs of superomarginals in the proximal half of one arm, but in another arm they are only present between the first three pairs of superomarginals. They may also be found scatteredly far out in the arms, though never between the last few pairs of joining plates.

Both large specimens from st. 280, with R/r 84/22 and 86/24 mm, show arms without a single supplementary dorsal plate, besides an arm in which there is a continuous series of small dorsal plates, reaching almost to the terminal ossicle. Also small specimens, e. g. one with R/r 20/10 mm, may have a continuous series of small dorsal plates for almost the whole arm length (fig. 10*c*). This character thus is not one of age. Secondary dorsal plates occur in most specimens only in the proximal part of the arms.

The presence of such a series of supplementary dorsal plates in the arms was, as mentioned above, considered the character distinguishing *T. magnus* from *T. cylindratus*. That it is of no taxonomical value, however, is evident from the variation met with in the present material.

The terminal ossicles in the specimen with R/r 87/23 mm are small but fairly conspicuous since they, so to speak, ride on the arm ends, covering the outermost two or three pairs of rudimentary superomarginals. One has 3 small conical spines preserved on its distal end around the end of the furrow (fig. 10*h*), whereas the others appear naked. Along their proximal margin the terminal ossicles bear a row of minute spinelets like those on the marginal plates, and minute spinelets may also occur on their main surface. Seen from the side the terminal ossicles are high, subcircular, seen from above they show an oval contour.

This appearance of the terminal ossicles is the usual for medium-sized specimens, but the number of spines around the furrow end may be larger. There may be two additional pairs of subequal subterminal spines and further a few spinelets to each ventral side of the ossicle (or in other words up to 5 pairs of subterminal spines or spinelets). Possibly there may also be a few spinelets distally on the lateral sides, and occasionally there may also be an additional unpaired dorsal spine, close to the terminal one. In these medium-sized specimens the terminal ossicles are of about the same width as the arm-ends. In the large specimens the terminal ossicles become relatively smaller in relation to the arm ends which increases in thickness with age so that the terminal ossicle in a large specimen may be only

Fig. 11. *Thoracaster cylindratus*. a-d) St. 314, R/r 54/21 mm; b, arm angle in dorsal view, the odd superomarginal plate is the second from the left; c, paxillae and papulae in four times the usual scale. e-h) St. 238, R/r 89/28 mm; e-f, same arm in lateral view and in dorsal view; h, inferomarginals nos. 1-3 in ventral view. i-o) St. 238 R/r 100/27 mm; i-j, two groups of paxillae in lateral and dorsal view respectively; k, jaw in ventral view; l, another jaw in lateral view; m, arm base in dorsal view, showing the superomarginals nos. 7-9; n, same in lateral view; o, distal end of same arm. p-r) St. 232, R/r 101/30 mm; q, adambulacralia nos. 10-11; r, adambulacralia nos. 33-35. s) St. 238, R/r 103/30 mm, distal end of arm.
Scale: 10 mm (in c, i and j: 2.5 mm).

half as broad as the end of the arm, and when seen from the side, often almost hidden by the superomarginals, which have grown up around it.

This excessive development of the distal superomarginal plates probably is a consequence of senescence, the growth of the arms in length by the interpolation of new superomarginal plates at the terminal ossicle having stopped. A size of R/r about 100/30 mm then may be about the maximum-size attained by the species. In the large specimens the terminal spines also often seem to disappear. In the juvenile specimens the terminal ossicles are wider than the arm ends, broader than long, and with a concave proximal margin. With increasing age the terminal ossicles grow longer, their proximal border becoming straight in specimens with R about 15-20 mm, and the ossicle having its final appearance in specimens with R about 25 mm.

The whole dorsal area of the disk is covered with close-set paxillae (figs. 10*j, r;* 11*i-j*). In the specimen with R/r 87/23 mm the paxillae are mainly oval in outline in radial direction and bear on the average 12 spinelets (18 being the largest number of spinelets counted). Centrally on the disk the specimen shows an apical cone with smaller paxillae with only 2-3-4 spinelets.

In the juvenile specimens available, the number of spinelets to each paxilla is 2-3-4 in one with R/r 13/7 mm, and about 4-6 and up to 10, respectively, in two other specimens of the same size. The largest number of spinelets to a paxilla is about 12 in some specimens with R/r ranging from about 25/10 to 42/12 mm, but about 15 in some others of the same size. Specimens ranging from R/r 66/23 mm to the largest ones on record, may have about 20 spinelets to a paxilla as the largest number. The large specimen from st. 232 with R/r 101/30 mm thus has mainly 12-16 spinelets to each paxilla, and 21 as the largest number counted. Other specimens with R/r 60/20 to 86/24 mm have paxillae with up to 25 spinelets, and still others with R/r 54/21 mm or more, have paxillae with up to about 30 spinelets. As many as 33 spinelets were counted on a paxilla of a specimen with R/r 70/24 mm.

All paxillae in the same specimen are subequal in height. The shafts in the smaller paxillae are therefore higher than wide, whereas in the larger ones they are about as wide as high. Very often the paxillae are suboval in outline and in general they are arranged with their larger diameter in radial direction.

The juvenile specimens are provided with a distinct, though short apical appendage, and an apical appendage may also be found in specimens as large as with R/r 31/11 mm. Larger specimens may show a more or less distinct apical cone, e.g. the two specimens from st. 280 with R 84 and 86 mm. Also the one from st. 232 with R/r 101/30 mm show a faint apical cone. Usually, however, the large specimens have no apical cone formed, having the central area of the disk marked off only by a number of small paxillae, i. e. with a crown of only a few spinelets and a slender shaft, but in height subequal to the other paxillae of the disk.

Papulae were only discernible in a few specimens which were especially well expanded. In one of the largest specimens they were found extending into the arm bases to either side of a 3-4 paxillae broad area radially.

The madreporic body has the striae stretching across in radial direction or radiating from an adcentral point. In the large specimens it is fairly inconspicuous, of a diameter about equal to the length of the adjoining marginals or somewhat less, and separated from these by a few rows of paxillae.

The adambulacral ossicles number 38 in the specimen with R/r 87/23 mm. The proximal ones carry in general 4-5 subequal furrow spines, but 6 furrow spines may be found on some ossicles, also among the distal ones. The proximal adambulacralia are subrhomboid in contour, but from about the sixth ossicle their shape changes, and they gradually become more narrow, especially their distal end narrowing down to give room for the podia. In the arms the interradial margin of the adambulacralia becomes curved, and the ends of the ambulacral ossicles are exposed. The furrow spines are subequal, and on the proximal adambulacralia arranged in a continuous series, whereas on the more distal ones the aboral furrow spine becomes placed on the narrow part of the ossicle at a small distance from the other 3-4 ones on the adoral half or two-thirds of the margin.

The furrow spines appear rather slender conical or spindle-shaped, though more or less flattened in vertical direction and with a short and somehat broader basal part marked off by a faint constriction. This basal part is imbedded in the strong web which connects the whole series of adambulacral and oral spines (figs. 10*m, t,* and 11*g, p*).

On their surface the adambulacralia in the specimen with R/r 87/23 mm are provided with a number of subambulacral spinelets; on one of the proximal ossicles e. g. 7 arranged in two irregular longitudinal series. The subambulacral spinelets are subequal on the proximal ambulacralia, but from about the sixth ossicle, the most aboral one becomes larger than the others, reaching the same size as the furrow spines. Of the other 4-8 subambulacral spinelets, two are generally placed at the adoral margin of the ossicle and the others in an irregular longitudinal series between these and the large aboral spinelet.

A number of 4 or 5 adambulacral spines appear to be equally frequent in the specimens available, also in the juveniles. The specimen with R/r 13/7 mm has 3 furrow spines on some of the ossicles in the arms, but otherwise the number is 4. A few specimens, also some small ones, have 6 furrow spines on some ossicles. One of the largest specimens, R/r 100/27 mm, has 5 furrow spines as the most common number, but on some ossicles it has 6, and on the proximal ones occasionally even 7 furrow spines.

The number of adambulacral ossicles is 11 in a specimen with R/r 13/7 mm and 6 paired superomarginals, 14 in one with R/r 14.5/7 mm and 8 superomarginals, 21 in one with R/r 26/11 mm and 12 superomarginals, 22 in one with R/r 31/11 mm and 14 superomarginals, and 40 in one with R/r 101/30 mm and 28 superomarginals.

The oral ossicles are fairly inconspicuous since their surface is more or less level with that of the ventrolateral area, and since the suboral armature of spines fairly gradually pass into the ventrolateral spine armature. In the specimen with R/r 87/23 mm the oralia carry marginally 8 spiniform spines, the proximal one slightly larger than the others, which are subequal in size. On their surface the oralia are provided with about 20 fairly uniformly spaced spines, thus along the sutural edge a series of about 8 which gradually decrease in length from the proximal to the distal one, the proximal spine in the series being close to and of about the same size as the enlarged proximal oral spine; on the main surface up to 6 spines, the largest of which are subequal to the marginal spines, and further some few additional suboral spines or spinelets near the distal margin.

The oral armature of the medium-sized and larger specimens agree with the above description (cf. eg. fig. 11*d, g*). The number of suboral spines increases with age, whereas the number of marginal oral spines is about the same in the smallest as well as in the largest specimens available. In a juvenile specimen with R/r 13/7 mm the usual number of marginal oral spines is 6, but 7 occur on some ossicles. Another juvenile specimen with R/r 15/7 mm has 7-8 marginal oral spines. The larger specimens, inclusive of the largest present, generally have 7 or 8 marginal oral spines, but a few large specimens have a marginal series of 9 spines on some oralia, and also a specimen with R/r 60/21 mm has 8-9 such spines. The proximal oral spine usually is about twice as large as the others, but sometimes it is only slightly larger. In the juvenile specimen with R/r 13/7 mm there may be only 4 suboral spines; in the specimen with R/r 14.5/7 mm there are 5-6, and in one with R/r 26/11 mm 6-7 suboral spines. A specimen with R/r 89/28 mm has 16-20 suboral spines, and the largest specimens with R about 100 mm (fig. 11*p*) have about 15 to 24 suboral spines and spinelets on each ossicle.

The primary oral ossicle is not very conspicuous. It has a naked surface in the specimen with R/r 87/23 mm, but in other specimens it is often armed with one or a few spinelets similar to the small suboral ones and to those of the ventrolateral area.

The ventrolateral area is closely paved with overlapping small plates (their adoral border free). The specimen with R/r 87/23 mm has 3-4 ventrolateral plates in the first tangential row at the oralia, and each of these plates carry up to about ten slender spinelets, distributed all over the surface of the plates though mainly along their proximal border. The median ventrolateral plates carry about 4 spinelets, all placed at the adoral edge, and the most distal and smallest plates, 8 of which about correspond with a marginal plate, carry only a single spinelet each. Small ventrolateral plates occur in the present specimen out in the arms to the inferomarginals nos. 20-22.

A radiating arrangement of the slightly transversely elongate or subhexagonal ventrolateral plates may be rather distinct in the juvenile specimens. In the large specimens these plates become so crowded however, that only the tangential and longitudinal arrangements are perceptible. The ventrolateral plates in the large specimens are further concealed by a fairly thick integument. Often there are only two ventrolateral plates in the first tangential row, and each of these plates may carry up to 15 spinelets in the largest specimens. About 8 ventrolateral plates, with single spinelets, correspond also in the largest specimens with a marginal plate. Generally the ventrolateral plates extend almost to the end of the arms, in the large specimens in several series. In the specimen with R 100 mm and 26 inferomarginals, ventrolateral plates thus are present to the 18th or 19th inferomarginals.

Distribution:

Thoracaster cylindratus is hitherto known from 19 dredgings in depths ranging from 2600 to 4990 m (11 of them in depths exceeding 4000 m). Six of the dredgings were in the eastern and tropical Atlantic, eight in the northern Indian Ocean, and five in the eastern tropical Pacific. (Fig. 33). Specimens of *Thoracaster* are further collected by the Vitjaz in the western North Pacific (Kurile-Kamchatka Trench) in about 4000-5000 m. *Thoracaster cylindratus* has been found on a bottom of globigerina ooze, calcareous clay, and white, grey, yellowbrown, green, or black mud, at temperatures between 1.3° and 2.8°C.

Styracaster Sladen, 1883

Type-species: *Styracaster horridus* Sladen, 1883.

Syn.: *Machairaster* E. Perrier, 1884 (type-species: *Machairaster pictus* E. Perrier, 1884 = *Styracaster spinosus* E. Perrier, 1885).
Chunaster Ludwig, 1907 (type-species: *Chunaster scapanephorus* Ludwig, 1907 *Styracaster horridus* Sladen).

Diagnosis:

Porcellanasterids with superomarginals forming a complete casing to arms. A varying number of erect spines in arm midline. Superomarginals of disk unarmed. A mid-interradial suture. Cribriform organs (3-11) confined to marginals of disk.

Description:

The disk is pentagonal. The arms are well set off, narrow, tapering and more or less compressed. Their length varies considerably in the different species. R is known to reach a length of almost 150 mm in some species; and in some large specimens the ratio R/r may exceed 6. In one species, however, the ratio R/r may be less than 2 even in adult specimens. The body is flat when the stomach is empty, and neither is it very tumid when the stomach is full. The terminal ossicle is fairly conspicuous and rather distal to the arm end. The whole dorsal side may be uniformly covered with well developed paxillae, but in some species there is a pavement of naked plates at the arm bases, and in others there are no paxillae at all, but only spiniferous plates. The jaws show a prominent keel formed by the interradial part of the two combined oralia, which are separated by a suture of varying width, meeting proximally and usually also medially, but this latter not in all species. The primary oral ossicle has a triangular surface well exposed. The oralia carry a varying number of marginal spines, the proximal of which is the largest. The elongate adambulacralia of the main part of the arms show a protruding adoral part with a varying number of furrow spines, and an incurved aboral part, either naked or with a single isolated furrow spine. The ventrolateral area has a pavement of plates, naked or with scattered granules. The surface of the oralia, and the adambulacralia, may likewise be either naked or provided with a small number of granules or spinelets.

Remarks:

Sladen (1883) erected *Styracaster* to comprise his two species *horridus* and *armatus*, and several other species have later been ascribed to the same genus, viz. *spinosus* and *edwardsi*, by E. Perrier in 1885, *clavipes* by Wood-Mason & Alcock in 1891, *chuni*, *caroli*, *monacanthus*, and *paucispinus*, by Ludwig in 1907, and *elongatus*, and *robustus*, by Koehler in 1907 (*a* and *b*). Further Lieberkind in 1935 described a new subspecies: *chuni* var. *groenlandica*. The specimen mentioned as *Styracaster* sp. by Chun in 1900, was by Ludwig in 1907 described as representing a new genus and species, *Chunaster scapanephorus*, which, however, is identical with Sladen's *Styracaster horridus*. The form which E. Perrier in 1884 referred to as *Machairaster pictus* is the same as he later called *Styracaster spinosus*.

A total of 12 species has thus been described in the genus *Styracaster* (inclusive of *Chunaster*), and presumably most of them are valid. The Galathea Expedition collected 54 specimens of *Styracaster* in all, representing 5 different species, all previously described; and this fairly large material has made it possible to undertake a comparative study of the species of the genus, and to form an idea of the infraspecific variation, and also to evaluate the characters distinguishing the different species.

Juvenile specimens of *Styracaster*, in *S. horridus* e. g. up to a size of R about 30 mm, have still only poorly developed dorsal paxillae even if the adult specimens have dorsal paxillae crowned with a large number of spinelets. The present author in 1951 ventured, therefore, to set forth the opinion that some of the species of *Styracaster* described as being without real paxillae, would prove to be based on juvenile specimens, and the character of their dorsal armature thus be of no taxonomical value. The present study has, however, disproved this supposition. A specimen of *S. armatus* in the Galathea material clearly shows that SLADEN based his description of this species on an adult specimen. The type-specimens of E. PERRIER's *S. spinosus* and *S. edwardsi* were small, considering the size attained by such species as e. g. *S. horridus* and *S. elongatus*, but later material of *S. spinosus* has shown that pseudo-paxillae with only single spinelets are found also in the full-grown specimens. (Incidentally, *S. spinosus* and *S. edwardsi* are almost certainly synonymous).

The species of *Styracaster* (some of them perhaps only nominal) may be grouped as follows:

1) A group symbolized by the type-species *S. horridus* (of which *Chunaster scapanephorus* is a synonym), and further comprising *S. caroli* and also *S. elongatus*. These three species are well distinguished.

2) A group symbolized by *S. chuni*, and comprising also *S. paucispinus*, and further *S. robustus*.

3) A group symbolized by *S. armatus* and comprising also *S. spinosus* (with which *S. edwardsi* is almost certainly identical), and the uncertain *S. clavipes* (perhaps also identical with *S. spinosus*). – The taxonomical status of the forms in this group thus is not yet quite clear.

Finally *S. monacanthus* may be ranged in a group of its own, but apparently near that of *S. armatus*.

Key to the species of *Styracaster*

			Page
1a.	A dorsal armature of well developed paxillae		2
1b.	A dorsal armature of imperfect pseudo-paxillae or spiniferous plates		7
2a.	Arms comparatively short, R ≦ 3 r. Distal terminal spine conspicuous		3
2b.	Arms long. R > 3 r to 5 r. Distal terminal spine not especially conspicuous. Whole disk area uniformly covered with paxillae		5
3a.	A triangular area of naked plates at arm bases		4
3b.	Whole disk area uniformly covered with paxillae	*robustus*	119
4a.	Adambulacralia of arms with 2-3 pointed conical furrow spines on adoral protruding half, and an adoral subambulacral spine	*chuni*	113
4b.	Adambulacralia with about 5 flattened furrow spines, no subambulacral armature	*paucispinus*	118
5a.	Inferomarginals of arms more than half as high as accompanying superomarginals. An aboral subambulacral spine	*elongatus*	110
5b.	Inferomarginals of arms less than half as high as accompanying superomarginals. An adoral subambulacral spinelet or granule		6
6a.	The aboral spine the largest in the furrow series. The adoral furrow spines possibly modified as segmental papillae. Lateral oral spines flat, subcircular	*horridus*	93
6b.	The aboral spine the smallest in the furrow series. Furrow spines and lateral oral spines all pointed, conical	*caroli*	107
7a.	A triangular area at arm bases with naked larger plates. R about 3 r		8
7b.	Whole dorsal side uniformly covered with spiniferous plates or pseudo-paxillae. Arms very short and narrow. R ≦ 2 r	*monacanthus*	123
8a.	Oralia in the pair forming a jaw only meeting proximally	*armatus*	119
8b.	Oralia in the pair forming a jaw also meeting medially, at the primary oral ossicle	*spinosus* (and *clavipes*)	121, 123

Styracaster horridus Sladen, 1883
Figs. 12-17. Pls. VII-VIII.

Styracaster horridus n. sp., SLADEN 1883 pp. 229-232; 1889 pp. 150-152, pls. 23_{5-7}, 27_{17-20}.
Styracaster horridus, KOEHLER 1909*b* pp. 38-39.
Styracaster horridus, KOEHLER 1921 p. 2.
Styracaster horridus, MADSEN 1951 pp. 78-80, fig. 2.
Styracaster sp. LUDWIG, in CHUN 1900 p. 288, fig.
Chunaster scapanephorus n. sp., LUDWIG 1907 pp. 316-317.
Chunaster scapanephorus, LIEBERKIND 1932 pp. 288-291, textfig. 11, pls. 1_7, 5_{1-3}, 6_{16-18}, 7_4.
Chunaster scapanephorus, MADSEN 1951 pp. 80-81.
Non: *Styracaster horridus*, WOOD-MASON & ALCOCK 1891, ALCOCK 1893 = *S. caroli* Koehler, 1907.
Nec: *S. horridus*, RICHARD 1903, = *S. elongatus* Koehler, 1907.

The type-specimen of *Styracaster horridus* was collected by the Challenger in the tropical eastern Atlantic (st. 346: 2°42′S, 14°41′W, 4298 m, globigerina ooze, 1.1°C.), and it appears from SLADEN's text that at least one other larger specimen was at disposal. (WYVILLE THOMSON (1877 pt. II p. 267) noted from the haul "three fine specimens of a new species of *Porcellanaster* remarkable for a series of long spines running along the centre of the back of each ray".)

The type-specimen has R/r 75/15 mm; 23 superomarginals, all longer than high, and according to the figure joining their opposites from plates no. 4. A continuous series of erect slender sharply pointed spines along midline of the laterally compressed arms, borne generally on alternate plates of all successive pairs of opposite superomarginals. Proximal arm spines longer than height of arms, towards arm tips decreasing fairly regularly in lenght. Inferomarginals about twice as long as high. 7-9 papilliform cribriform organs. Terminal ossicle rather compressed, elongate in contour (dorsal to about two rudimentary superomarginals), with 3 spines, a terminal one and a pair of subterminal ones (in a large specimen possibly with an additional spine in the dorsal midline). Dorsal side of disk with closely crowded small pseudo-paxillae with 4-8 spinelets. Adambulacralia elongate, subrhomboid, with furrow margin and ventral side incurved, proximal ossicles with 5 subequal short flat and pointed furrow spines, those of arms with 3 short slightly compressed and sharply pointed spines on adoral part of furrow margin, and a much longer and pointed spine on aboral part. (In large specimens 1-3 adorally placed subambulacral granules). Oralia with a pointed conical spine on tip (or two such spines, one above the other), and a series of 7-8 subequal short and flat spines along lateral margin. (In a large specimen 4-5 suboral granules in a series along median suture). Ventrolateral area with transversely elongate plates with spaced irregularly placed granules.

KOEHLER in 1909 records two specimens of *Styracaster horridus* dredged by the Princesse Alice in the Bay of Biscay and east of the Azores respectively (st. 757: 44°06′N, 10°22′W, 4900 m, muddy ooze; and st. 1789: 31°06′N, 24°00′W, 5413 m). R/r are ?/22 and 34/9 mm. The smaller specimen has 15 superomarginals, 5 cribriform organs, only few arm-spines, and in most cases only 3 adambulacral spines.

In 1921 KOEHLER records three additional specimens from three other dredgings of the Princesse Alice, all in the Bay of Biscay (st. 2986: 45°08′N, 7°06′W, 4870 m; st. 2994: 44°08′N, 10°44′W, 5000 m; and st. 2997: 44°29′N, 10°31′W, 4965 m).

Finally the present author, in 1951, described three juvenile specimens of *Styracaster horridus* from a dredging made by the Swedish Deep-Sea Expedition in the tropical Atlantic near the type-locality (st. 329: about 9°44′N, 26°25′W, 5610-5600 m, calcareous red clay, 2.4°C.). The specimens in question had R/r 30/8, 23/7, and 13/5 mm, and 15-17, 13-15, and 11 superomarginals respectively. The largest one agreed fairly well with the type, whereas the two smaller ones were still without paxillar spinelets and had only a few arm-spines (one of these always on the first pair of joining superomarginals).

Styracaster horridus was also recorded from the Indian Ocean by WOOD-MASON & ALCOCK (1891), but according to KOEHLER (1909*a*), who has re-examined these author's material, the specimens in question actually belonged to *Styracaster caroli*.

Chunaster scapanephorus: This genus and species was briefly diagnosed by LUDWIG in 1907 on the basis of a specimen collected by the Valdivia Expedition in the Indian Ocean south of Sumatra (st. 183: 8°14′S, 98°22′E, 5248 m, radiolarian ooze), and previously (on basis of LUDWIG's preliminary identification of it) listed as *Styracaster* sp. by CHUN (1900), who also published a photograph of it. The same specimen was subsequently given a more detailed and fully illustrated description by LIEBERKIND in 1932.

The type-specimen of *Chunaster scapanephorus* has R/r 98/27 mm; 24-30 superomarginals, longer than high, joining their opposites from plates no. 6. Along the midline of the laterally compressed arms a series of 11-14 erect slender pointed spines, one to each pair of joining superomarginals, proximally at least as long as the arm is high, more or less regularly decreasing in length towards the arm ends. Inferomarginals of disk subrectangular, of arms four times as long as high; 11 cribriform organs. Terminal ossicle laterally compressed, with 3 spines. Whole dorsal side with close-set paxillae with 4 (-6) spinelets. Adambulacralia of arms elongate, with an incurved furrow margin, adorally with a series of (3-) 5 spatulate furrow-spines in a common web, and aborally with a larger conical pointed spine. Proximal 3-4 adambulacralia relatively shorter, with a continuous series of 9-10 spatulate furrow spines, and further with up to about 5 subambulacral granules on adoral surface. Oralia each with a stout conical spine at tip, and laterally with a series of 9 (-10) spatulate marginal spines similar to adambulacral ones; also a suboral granule. Ventrolateral area paved with proximally spaced, and distally close-set and in radial series arranged plates with scattered granules. Minute ventrolateral plates extending in about a double series almost to terminal ossicle.

If this description is compared point by point with that of the type-specimen of *Styracaster horridus,* it appears that the only character by which *Chunaster scapanephorus* is distinguished is in the presence of ventrolateral plates in the arms, almost to the arm end. The larger number of cribriform organs in *Chunaster scapanephorus* is accounted for by the larger size of this specimen, and the peculiar adambulacral armature, which LUDWIG and LIEBERKIND emphasize as especially characteristic of the form, really is exactly identical (and also identically described) in *Styracaster horridus.*

The Swedish Deep-Sea Expedition collected in the tropical mid-Atlantic, (st. 342: about 1°N, 18°40'W, 5250-5300 m, globigerina ooze, 2.3°C.) quite near the type-locality of *Styracaster horridus*, six porcellanasterids which the present author in 1951 recorded under the name of *Chunaster scapanephorus,* since they had a series of ventrolateral plates in the arms and also in all other characters agreed well with the description of this form given by LUDWIG and by LIEBERKIND. They had R/r ?/11, 52/12, 52/14, 51-55/16, ?/17 and 58/17 mm; about 18-19 superomarginals, joining from nos. 5-6; and 10-14 arm spines. Terminal ossicles sometimes with a fourth spine in the dorsal midline. (See fig. 13*f-i*).

Since these two named forms, *Styracaster horridus* and *Chunaster scapanephorus,* differ between themselves merely in the extent to which a ventrolateral armature of plates is developed in the arms, whereas in several of their other common characters they differ markedly from the other species described of *Styracaster,* they cannot possibly be generically different. Now, the possession of ventrolateral plates in the arms might be a character of specific or subspecific importance. But the material from the Galathea Expedition to be described below shows a so diverse armature of ventrolateral plates in the arms that it cannot be considered of any taxonomic importance specifically; no more than could e. g. the armature of secondary dorsal arm plates in *Thoracaster.*

The Galathea material:

A total of 24 specimens and some fragments of *Styracaster horridus* were dredged at seven stations: in the Atlantic in the Gulf of Guinea, in the Indian Ocean off Tanganyika and south of Ceylon, and in the South Pacific in the Kermadec Trench north of New Zealand, respectively.

St. 30: 0°42'N, 5°59'W, 5160 m, 2.2°C., clay. 10 specimens.
St. 234: 5°25'S, 47°09'E, 4820 m, 1.8°C. 3 specimens.
St. 235: 4°47'S, 46°19'E, 4810 m, 1.4°C., globigerina ooze. 1 specimen.
St. 282: 5°32'N, 78°41'E, 4040 m, 1.5°C., blackish mud. 2 specimens.
St. 663: 36°31'S, 178°38'W, 4410 m, 1.2°C., brown, sandy clay. 2 specimens.
St. 664: 36°34'S, 178°57'W, 4540 m, 1.1°C., brown, sandy clay. 6 specimens + fragment.

All the specimens available from the Atlantic and the Indian Ocean have the characteristic adambulacral armature described for the types of *Styracaster horridus* and *Chunaster scapanephorus.* The material of two specimens from st. 282, south of Ceylon, agrees with the type of *Styracaster horridus* in the absence of a ventrolateral skeleton in the arms, whereas the other material, from off tropical West Africa and off tropical East Africa respectively, in every population includes specimens corresponding closely to the one described as *Chunaster scapanephorus,* in having ventrolateral plates extending into the arms. It has been found most convenient, therefore, to describe the specimens from st. 282 separately. Also the specimens from the two dredgings in the Kermadec Trench in the South Pacific, will be dealt with separately, since they differ somewhat from the other specimens by having a more simple adambulacral armature.

The specimens from st. 282:

The two specimens representing the population of *Styracaster horridus* found in this locality, south of Ceylon, have R/r 91/21 and 85/15 mm respectively. The larger one in general appearance agrees well with the type-specimen of *S. horridus,* having the arms armed with 11-13 dorsal spines, whereas the smaller one shows a very different appearance, as it has only a single dorsal spine on each arm (always belonging to the first pair of joining superomarginals). This specimen thus does not at all correspond to the name of *horridus*. The specific identity of the two specimens, however, is beyond doubt, and, as will appear from the following, such an occurrence of one-spined specimens in a population of otherwise many-spined ones is known e. g. also in the species *Styracaster chuni*.

The specimen with R/r 91/21 mm (fig. 12*a-e, g-j, m*) has 30 superomarginal plates, which join from the fifth opposite pair. All marginal plates have a rather granulated surface. The superomarginal ones, of the arms as well as of the disk, are slightly longer than high, subrectangular if corresponding with their opposites and with the inferomarginals, but varying in shape to hexagonal if alternatingly arranged, which is a fairly frequent feature. Centrally the marginals show a faint depression.

The inferomarginal plates are in the arm angles about as high as the accompanying superomarginals, but proximally in the arms they are only about half as high, and distally only from one-third to one-fourth as high. In general they are of the same length as the corresponding superomarginals, but they may be shorter, so that e. g. 8 inferomarginals correspond to 5 superomarginals. In places the series of inferomarginals is interrupted by one or a few enlarged superomarginals reaching down to the ventral side.

The only two intact arms carry 11 and 13 dorsal spines respectively. The ten distal pairs of superomarginals are unarmed in both arms, and in one arm also the second, fifth, eight, and eleventh pair of joining superomarginals are without dorsal spines, whereas in the other arm it is the second, fourth, eighth and twelfth pair which are unarmed. The spine armature of these two arms is thus less developed than was the case in the type-specimen described by SLADEN. However, another, broken arm of the same specimen has a continuous row of dorsal spines on all the nine joining pairs of superomarginals left. In four of the radii in the present specimen there is another variation from the type-specimen, viz. that the most proximal arm spine (about 10 mm long) is developed already on the fourth superomarginal plate, which is completely separated from its opposite, whereas in the type (and in all other specimens described) the most proximal arm spine is always found on one of the plates of the first joining pair of superomarginals. The spines of the main (distal) part of the arms are slightly curved, with the point turned outwards, as was also noted by SLADEN for the type-specimen. They decrease more or less regularly in length as they proceed along the arm. (Fig. 12*e*).

The cribriform organs number 9 in each interradius in this specimen with R/r 91/21 mm. Each of the seven median ones, which consist of about 20-24 rows of papillae, covers a little more than one-third of each of the two sets of marginals on which they are developed. The series of covering papillae extends from one dorsal corner of the organ in a straight line almost to the ventral edge of the inferomarginal plate where it bends and continues near the margin and round to the other side of the organ, ending at the other dorsal corner. The outer cribriform organs, at the base of the arms, also reach almost to the ventral margin of the inferomarginals, from which they are demarcated by the series of covering papillae in the same way as are the median organs, but they do not reach to the dorsal side of the superomarginals.

The terminal ossicles have borne a fairly large spine at their tip, and further there is a pair of small subterminal spines. (Fig. 12*h*).

The whole dorsal area of the disk, inclusive of the arm bases, is covered with paxillae (fig. 12*m*), which usually are crowned by 6-7 spinelets, but sometimes have 8 or only 3-4 spinelets. This specimen with R/r 91/21 mm has the stomach filled to the utmost, and the whole disk area in consequence is much expanded, and the paxillae of the main part of the disk hence fairly spaced. (SLADEN's description of the shape of the disk in the type-specimen of *horridus* as not high, and the under surface convex, is of course an individual and not a specific characteristic). There is no apical cone. The dorsal integument is fairly thick and leathery, as noted by SLADEN. Papulae were not observed even though the specimen is well expanded.

The adambulacral ossicles number 45. Their armature consists on the proximal two to four ossicles (fig. 12*b, c*) of a furrow series with 4-5 blunt flat or spoon-shaped spines which as segmental papillae cover an oblong segmental pit, and further there are on the adoral part of the surface 2 or 3, sometimes 4 subambulacral granules. In the following adambulacral ossicles (fig. 12*d*) the aboral part narrows somewhat down to give room for the podia, and the furrow spines become pointed, and especially the distal one increases in length. The adambulacral armature in the arms (fig. 12*g, i, j*) then consists of a series of 3 (occasionally 4, and most distally only 2) flat and pointed spines on the adoral broad part of the ossicle, covering as segmental pa-

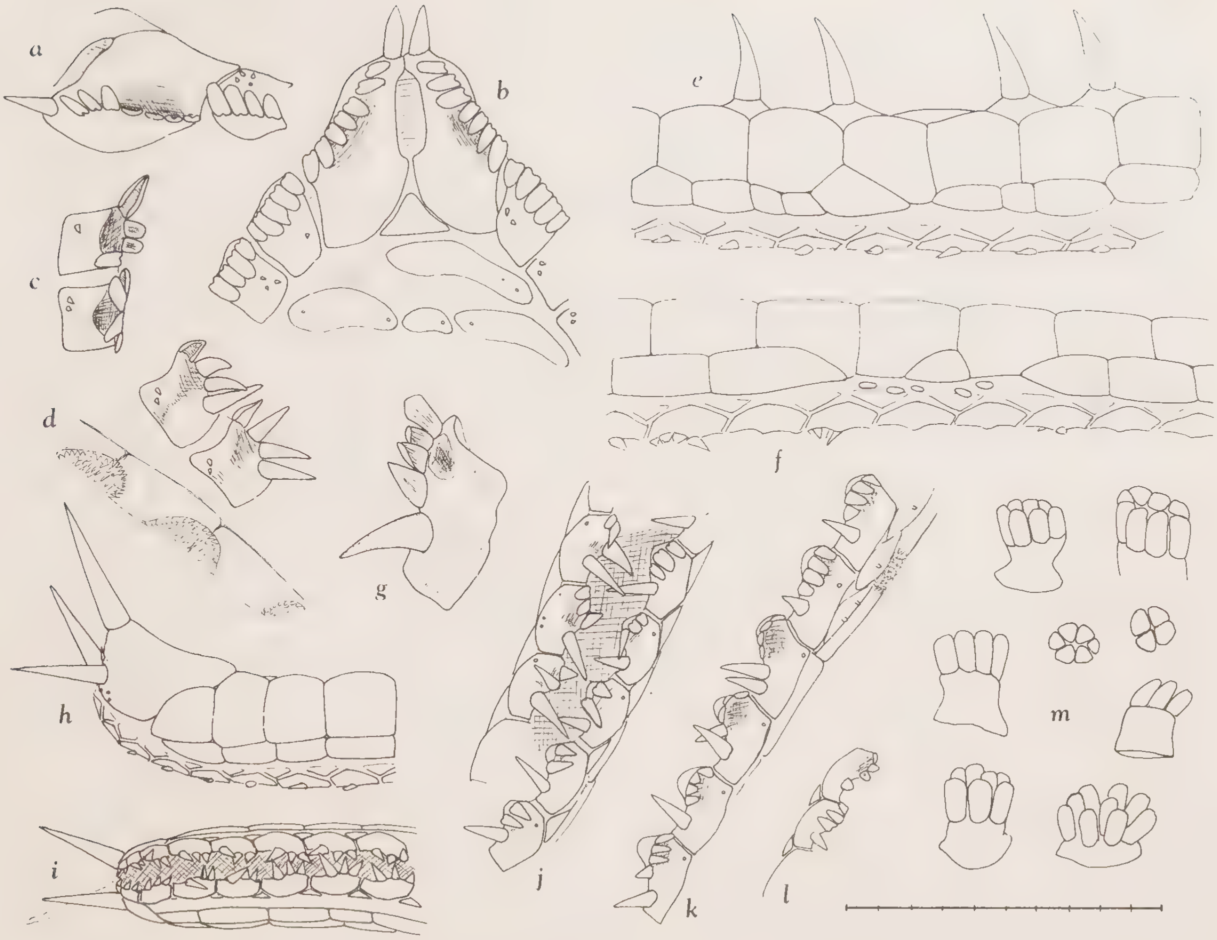


Fig. 12. *Styracaster horridus*, st. 282. a-e) R/r 91/21 mm (see also g-j and m); a, oral ossicle and first adambulacral ossicle in lateral view; b, another jaw in ventral view; c, adambulacralia nos. 3-4; d, adambulacralia nos. 6-7 and adjoining inferomarginals; e, part of arm, showing the superomarginals nos. 15-20, aboral end to the left. f) R/r 85/15 mm (see also k-l), part of arm, showing the superomarginals nos. 11-15, aboral end to the right. g-j) R/r 91/21 mm; g, adambulacral ossicle no. 15, seen obliquely from the side, in twice the usual scale; h-i, distal end of arm in lateral view and in ventral view; j, part of arm in ventral view, showing the adambulacralia nos. 22-26. k-l) R/r 85/15 mm; k, adambulacralia nos. 7-12; l, adambulacralia nos. 24-25. m) R/r 91/21 mm, paxillae in four times the usual scale.
Scale: 10 mm (in g: 5 mm, in m: 2.5 mm).

pillae a faint segmental pit, and of a spiniform pointed spine about as long as the ossicle, standing alone on the aboral narrow part at some distance from the adoral series. The more distal adambulacral ossicles carry further (always?) a single subambulacral granule near their outer adoral corner. The triangular ends of the ambulacral ossicles are distinctly visible in the arms (fig. 12*j*).

The prominent oral ossicles (fig. 12*a, b*) each carries a fairly large conical spine at the tip and along the margin a series of 8 about one-third as large, blunt and flat or spoon-shaped spines, which are to be described as a series of segmental papillae, and which cover a distinct, long segmental pit. The surface of the oralia is naked.

The ventrolateral plates are transversely elongate, arranged in about 6-8 tangential series, and distally also in radiating series, which two and two approximately correspond with an adjoining marginal plate. The proximal ventrolateral plates are about twice as large as the distal ones and more irregular, often rather boomerang-shaped with one part parallel to the furrow. The plates, especially the proximal ones, are fairly spaced, partly because the specimen is well expanded by a full stomach. They are covered with a fairly thick integument and each may carry up to half a dozen very minute granules. The ventrolateral plates are confined to the disk area. Only a narrow strip of naked skin extends between the series of inferomarginals and adambulacral ossicles.

The other specimen of *Styracaster horridus* from st. 282 (fig. 12*f, k, l;* pl. VIII 1-2) has R/r 85/15 mm by an empty stomach. There are 25 superomarginals, joining their opposites from the fourth or fifth pair, and 8-9 cribriform organs, which in places coalesce with their neighbour to one or to either side. The specimen, as already mentioned, is remarkable in having only a single dorsal spine to each arm (always placed on one of the superomarginal plates of the first pair of joining ones). The specimen, however, is otherwise slightly more spiny than the other one. The terminal ossicle is provided with two pairs of small subterminal spines besides the large distal spine. There are 9 lateral oral spines besides the conical proximal one. The proximal three adambulacralia carry 5-6 spatulate furrow spines, and the vertebra-like adambulacralia of the arms (fig. 12*k*) carry an adoral series of 4 spatulate spines besides the longer spiniform spine aborally. A single plate was found with 2 aboral spiniform spines. A few subambulacral granules or granuliform spinelets occur in a transverse row near the adoral margin of the ossicles. The paxillae carry 4-8, mainly 6 spinelets. The madreporite, separated from the margin by a single row of paxillae, is round, with the striae radiating from an adcentral point, and along the adcentral edge provided with an armature of spinelets similar to those on the paxillae. There is a faint apical cone.

Nor in this specimen do the ventrolateral plates extend outside the disk area. In one arm, however, a few inferomarginal plates are missing at the superomarginals nos. 12-14, and the correspondingly broader strip of integument stretching between the series of marginals and adambulacral ossicles includes here a small number of spaced minute plates.

The specimens from sts. 30, 234, and 235. (Figs. 13-15. Pl. VII):

The ten specimens of *Styracaster horridus* from st. 30 have R/r in mm as follows (with the number of superomarginals added in parentheses): 15/6 (10), 20/8 (10-11), 35/9 (16-17), 58/12 (19), 60/13 (18), 63/15 (21), 66/19 (21), 68/14 (17-18), 75/16 (23), and 81/17 (23-25) respectively. The three specimens from st. 234 have R/r 45/14, 118-128/18 mm, and 118-131/20 mm, and about 23, 32, and 32-37 superomarginals; and the single one from st. 235 has R/r 118-146/29 mm by a full stomach (pl. VII) and 25-32 superomarginals. The ratio R/r increases thus from 2.5 in the smallest specimens with R about 15-20 mm to about 4 in specimens with R 35-81 mm, or to about 5, as in specimens with R 75 mm or more, thus also in the largest specimen with R 118-146 mm, even to 6.5 as in one with R 118-128 mm, which latter specimen, however, had an empty stomach and the disk area contracted so that the interradii are excave.

The superomarginal plates are in general subquadrate, slightly longer than high, but they may be distinctly rectangular. Those of either side of the arm may stand just opposite each other clear to the terminal ossicle, but they may also alternate more or less regularly, in which case they may be pentagular, even hexagonal if they alternate also with the inferomarginals. All kinds of arrangements may be found in the different arms of the same specimen. An irregular alternating arrangement seems the most common. The inferomarginal plates correspond in number to the superomarginals, proximally in the arms being about half as high as these and distally about one-third as high. Out in the arms the inferomarginals may alternate with the superomarginals, and then become subpentagonal instead of rectangular. The marginal plates have a granulated surface, and the superomarginals a fairly marked central depression.

The superomarginal plates join their opposites in the arms from plates nos. 4-5 in both small and large specimens, and from plates nos. 5-6 in the largest one with R 146 mm.

Dorsal arm spines are present in a number of 2 in the smallest specimen (fig. 13*a*), R/r 15/6 mm and 10 superomarginals, and in a number of 3-5 in the other small specimen, R/r 20/8 mm and 11-12 superomarginals. The specimen with R/r 35/10 mm has up to 8 spines to an arm, and one specimen with R/r 45/14 mm has 7 spines on the only arm preserved (with about 23 superomarginals). Some specimens with R about 60 mm have between 10 and 17 dorsal spines on each arm, and the same variation in number of arm spines is also found in some specimens with R about 70 mm. One specimen with R 75 mm has 17 spines on three of the arms, and 18 and 19 spines respectively on the two other arms. The two large specimens with R 118-131 mm, and 32 and 37 superomarginals, have 16-19 arm spines, whereas the largest specimen, with R up to 146 mm but only 32 superomarginals, have 10-11 arm spines.

The dorsal arm spines are often developed more or less regularly on every second superomarginal plate, alternatingly on either side of the arm (thus a spine for each successive pair of joining superomarginals), but they may also stand on successive plates on the same side for the greater length of

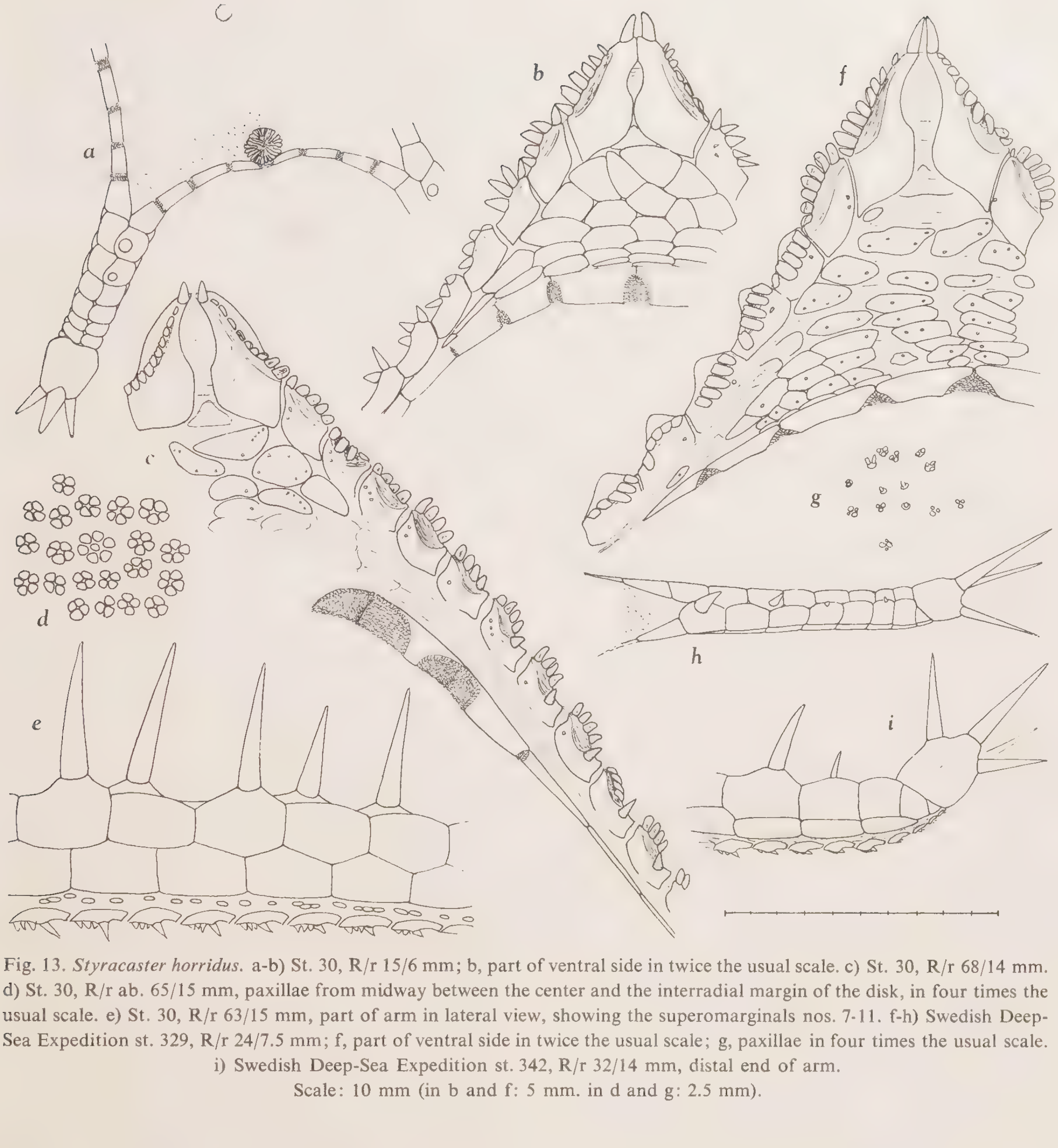


Fig. 13. *Styracaster horridus.* a-b) St. 30, R/r 15/6 mm; b, part of ventral side in twice the usual scale. c) St. 30, R/r 68/14 mm. d) St. 30, R/r ab. 65/15 mm, paxillae from midway between the center and the interradial margin of the disk, in four times the usual scale. e) St. 30, R/r 63/15 mm, part of arm in lateral view, showing the superomarginals nos. 7-11. f-h) Swedish Deep-Sea Expedition st. 329, R/r 24/7.5 mm; f, part of ventral side in twice the usual scale; g, paxillae in four times the usual scale. i) Swedish Deep-Sea Expedition st. 342, R/r 32/14 mm, distal end of arm. Scale: 10 mm (in b and f: 5 mm. in d and g: 2.5 mm).

the arm, and, more rarely, they may be present on successive plates on both sides of the arm for some distance, thus being placed very closely. The largest spines are usually found a little out on the arms, on the ninth or tenth superomarginals, and thereafter they decrease fairly gradually in length towards the tip of the arms. The largest arm spines measure e. g. 9 mm in a specimen with R 81 mm.

In the largest specimen available, R/r 146/29 mm, some scattered small rounded secondary dorsal plates of a size similar to the base of the spines, may be found inserted between the opposite superomarginals, mainly at the sutures between successive plates.

The number of cribriform organs in each interradius is 7 already in the youngest specimen with r 6 mm, very narrow ones, however. Also the medium-sized specimens have as a rule 7 cribriform organs in each interradius. A few specimens with R 60-75 mm and r 12-16 mm have 8 cribriform organs in one or more of the interradii. The specimen with R/r 85/15 mm has 8-9 cribriform organs. The specimen with R/r 118-128/18 mm, and the largest one, with R/r 118-148/29 mm, have 9 cribriform organs in each interradius, and that with R/r about 118-131/20 mm has 11 cribriform organs in some of the interradii. The median cribriform organs may be broadest at the horizontal suture, and possibly coalesce with their neighbours to one or to both sides.

The terminal ossicle (fig. 14*h*) is fairly high, laterally compressed, and carries in general 3 spines, a terminal one and a pair of usually slightly smaller subterminal ones (occasionally the unpaired terminal spine is the smallest). In the medium-sized and larger specimens the terminal ossicle may sometimes have an additional subterminal spine to one or to both sides of the furrow end. More rarely there is an additional fairly large spine proximally in the dorsal midline. In the largest of the present specimens the terminal ossicle of the only intact normal arm, R 146 mm (fig. 15*g, h*), is very enlarged in height, in ventrad direction (and has a third subterminal spinelet to one side). The whole appearance of this arm indicates that it has stopped growing normally in length, by adding new superomarginal plates, and the peculiar shape of the terminal ossicle in question may thus be interpreted as senescent.

The other arm preserved in this large specimen from st. 235 measures only 118 mm in length, but its outer end is lost in life, and instead of regenerating a new normal terminal ossicle, a substituting terminal end is formed by a pair, it seems, of opposite superomarginals, which have become somewhat thickened and provided with small spines (fig. 15*i, j*). A short distance before the arm end also an extra, similar immitation of a terminal end is formed, probably indicating another place of injury. A third arm in the same specimen is also in regeneration, and has hereby become forked, but during the dredging the distal ends of both forked parts are lost.

Paxillae cover the whole dorsal area of the disk, extending to the marginalia at the arm bases. In the smallest specimens, with R/r 15/6 and 20/8 mm, they are yet rudimentary, consisting only of small roundish plates (the later paxillar shafts) with only a single granuliform spinelet each. In the medium-sized specimens from st. 30, with R about 50-60 mm, the paxillae (fig. 13*d*) carry usually 4-5, and scattered ones as many as 7 granuliform spinelets. In the largest specimens (sts. 234 and 235) the paxillae (figs. 14 *l, m;* 15*b*) usually carry 4-7 spinelets, and scattered ones 8-9. Centrally on the disk there is an area with smaller paxillae, and there may be a faint apical cone, in the small specimens fairly distinct though low.

The madreporic body is roundish, generally with a diameter slightly larger than the length of the neighbouring marginals. It may be separated from these by a few rows of paxillae, but it may also be quite close to them, and pushing itself somewhat in between them in the interradial angle. The striae radiate from an adcentrally located point.

The adambulacral armature is poorly preserved in the two small specimens with R 15-20 mm, but apparently it consists in the main part of the arms of only 3 spines in general.

The proximal adambulacral ossicles in the other specimens with R 35 mm or more (figs. 13*c;* 14*d*) bear along their whole margin a continuous series of usually 5 (6-4) subequal flat spines, generally modified as distinct segmental papillae at a more or less distinctly developed, long, common segmental pit. (These segmental papillae have often the outer thinner calcareous part bent inwards at almost 90 degrees, which it is rather impossible to demonstrate in the drawings). The described appearance of the adambulacral armature changes gradually as one proceeds along the furrow, usually from about the fifth or sixth adambulacral ossicle, but sometimes (in the specimen with R 81 mm e. g.) not until about the tenth ossicles. First, the aboral furrow spine loses the spatulate appearance, becoming longer than the other furrow spines and pointed, the series of furrow spines on these more proximal ossicles still being continuous along the adambulacral margin; and a little farther out on the arms the aboral third of the adambulacral ossicle narrows down somewhat, and the larger aboral spine becomes placed by itself here, whereas the other spatulate furrow spines remain in a continuous row on the adoral part, as segmental papillae over a distinct segmental pit. In the distal half of the arms the difference in the aboral and adoral width of the adambulacral ossicles and the position of the spines becomes very pronounced, but here the adoral furrow spines are pointed and, except for their smaller size, similar to the aboral spine. The number of furrow spines on the distal adambulacralia is often 1-2 smaller than that found on the proximal ones, and thus there are only 3 (or 2) adoral spines besides the larger aboral one.

In some of the large specimens the armature of the more proximal adambulacralia may differ somewhat from what is typical, only the two most adorally placed furrow spines, or only the first, or none at all, being modified as segmental papillae, whereas the remaining spines are all spiniform and pointed like the aboral one, and only slightly decreasing in length from the aboral to the adoral end of the ossicles (fig. 15*d, f*).

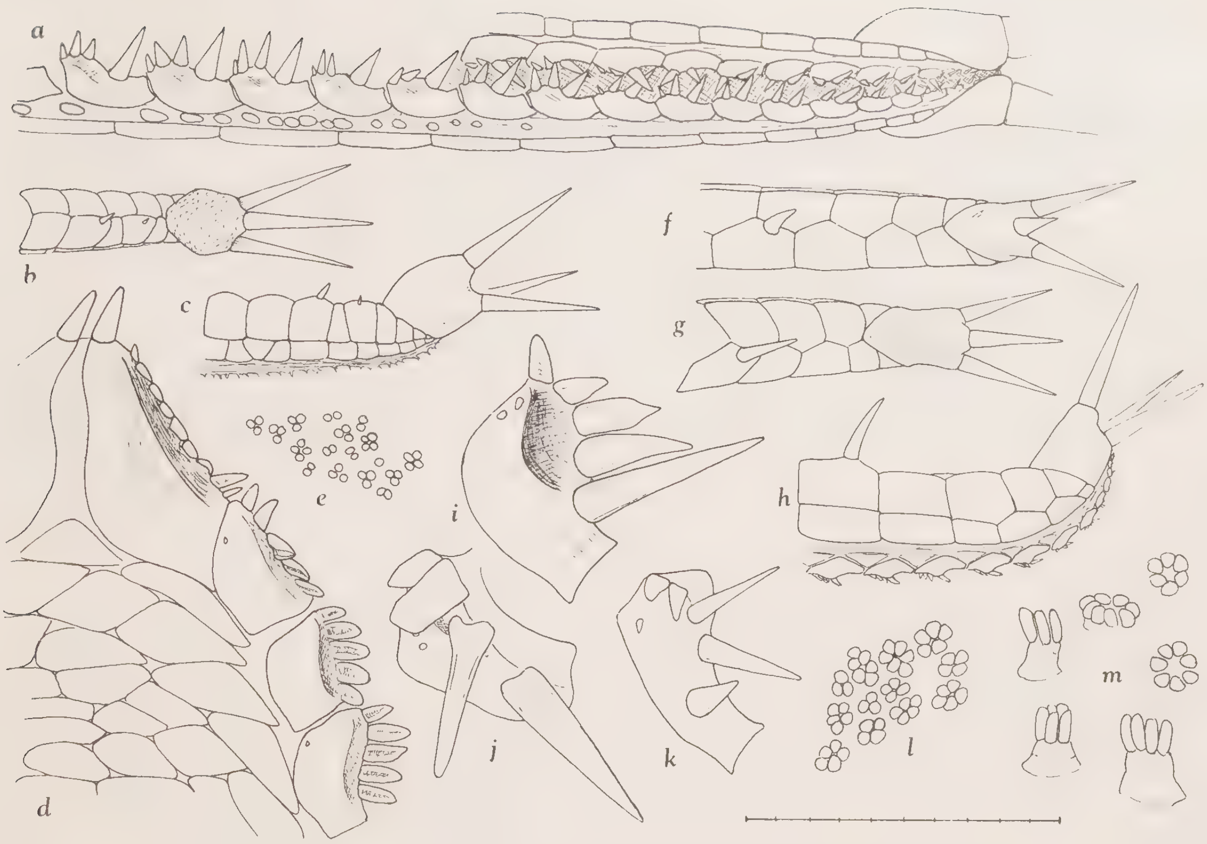


Fig. 14. *Styracaster horridus*. St. 234. a-e) R/r 45/14 mm; a, arm in ventral view in twice the usual scale; b-c, same in dorsal view and in lateral view; d, part of oral side in twice the usual scale; e, paxillae in four times the usual scale. f-m) R/r 118-128/18 mm; f-h, same arm in dorsal view, in oblique dorsal view (with the dorsal side of the terminal ossicle in the plane of the paper), and in lateral view respectively; i-k, adambulacralia nos. 8, 10, and 19 respectively, in twice the usual scale; l-m, paxillae in four times the usual scale.
Scale: 10 mm (in a, and i-k: 5 mm, in e, and l-m: 2.5 mm).

The flattened adambulacral spines (segmental papillae) of the more proximal ossicles, as noted above, have their outer part distinctly bent, and further the calcareous substance of this part is of a looser structure than the basal part, the feature being correlated with that the spines are enclosed in a sheat of skin which may extend far beyond their distal point. Lieberkind in 1932 p. 290, went into a detailed, but somewhat obscure discussion of these "spines", and so it may be worth while noting that in their whole structure they seem very similar to the aperture papillae of the pterasterids.

The surface of the adambulacral ossicles of the disk area and proximal part of the arms is provided with a varyingly developed armature, whereas the more distal adambulacralia have a naked surface (which sometimes may apply also to the proximal adambulacralia of the arms, e. g. even in the largest specimen, with R 146 mm). On the most proximal adambulacralia there may be a transverse row of up to 8 spinelets close to the adoral margin, or, more exceptionally, a disarranged group of up to half a dozen granules adorally. The adambulacralia of the inner part of the arms typically carry only 1-2 subambulacral spinelets adorally at the end of the segmental pit.

The ends of the ambulacral ossicles are visible in the whole arm length, simulating small triangular plates wedged in dorsally between successive adambulacralia.

The oral ossicles (figs. 13*c*, 14*d*) bear on their proximal tip a pointed somewhat flattened spine and along their lateral margin a series of about half as long subequal spatulate spines. The proximal spine e. g. is about 1 mm long in a specimen with R 60 mm. The number of marginal oral spines, inclusive of the larger one at the tip, is 7-8 in the smallest specimen with R/r 15/6 mm, and 9-10 in the other small one with R/r 20/8 mm. In the larger specimens the usual number of marginal spines is 10, but there may be 11 and sometimes only 9 marginal spines, the latter number e. g. also in a spec-

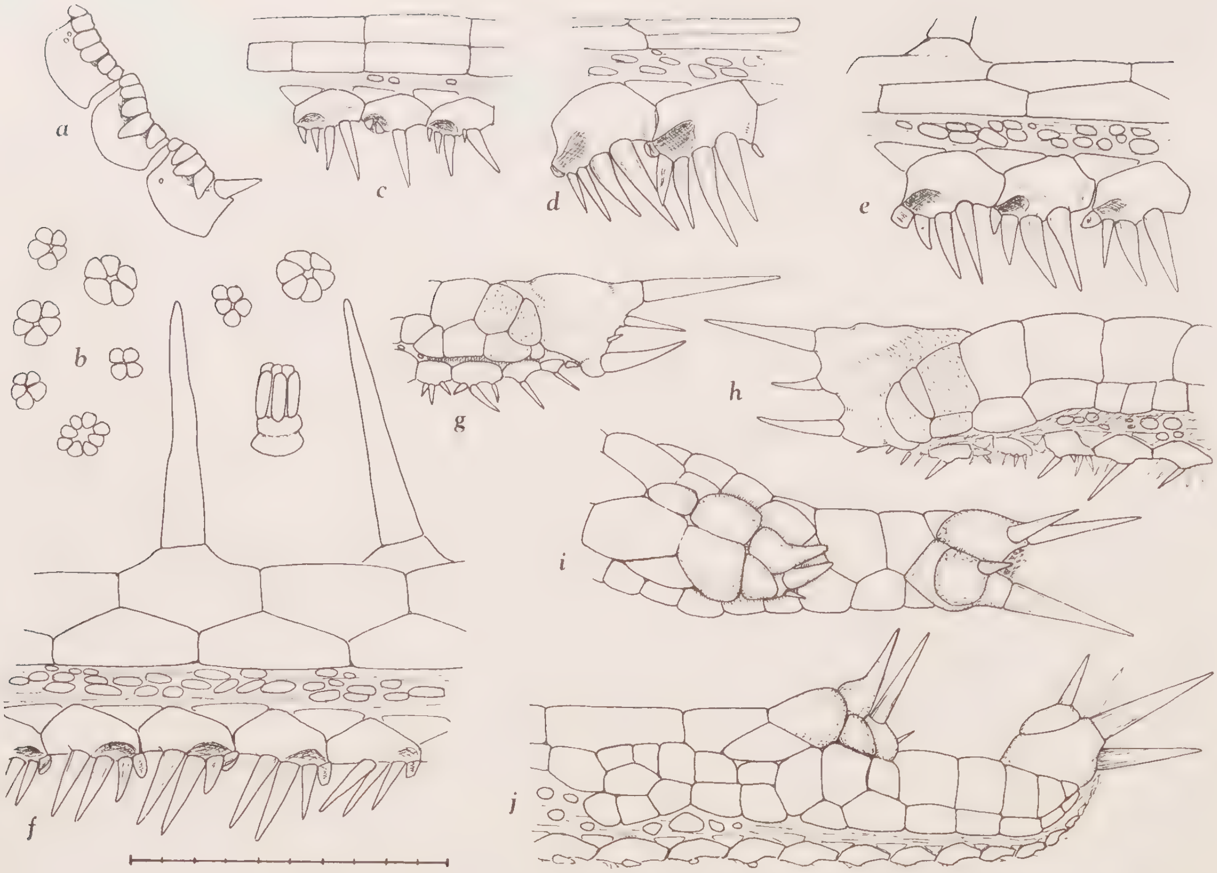


Fig. 15. *Styracaster horridus*. a, St. 234, R/r 128/18 mm, adambulacralia nos. 3-5. b-j) St. 235, R/r 146/29 mm; b, paxillae in four times the usual scale; c-e, parts of same arm in oblique ventral view (with the surface of the adambulacralia in the plane of the paper), showing: c, distal adambulacralia at inferomarginals nos. 25-26; d, proximal adambulacralia at inferomarginal plate no. 8; e, adambulacralia at inferomarginals nos. 13-14; f, part of same arm in lateral view (from the other side), showing the superomarginals nos. 13-14; g-h, distal ends of arms, with the granulated surface indicated on the terminalia and the distalmost marginalia; i-j, an abnormal arm in dorsal view and in lateral view.
Scale: 10 mm (in b: 2.5 mm).

imen with R/r 128/18 mm. Some specimens show in some radii different variations from the typical proximal oral armature of two larger spines, one to each ossicle of the pair forming a jaw. Thus 2 or even 3 of the proximal spines on each oral ossicle may be large and pointed, or there may be an additional unpaired spine between the two normal tip spines, or a jaw may have only such a single proximal larger oral spine, apparently common to the combined pair of oralia forming the jaw.

The surface of the oralia usually appear naked, but there may also be as many as 6 suboral spinelets in a scattered row along the suture and also (or instead) a few spinelets near the distal interradial margin.

The ventral exposed surface of the primary oral ossicle is equilateral triangular in contour.

The ventrolateral plates are transversely elongate and in the more distal part of the interradial area arranged in radiating rows, two and two about corresponding with an adjoining marginal plate. The ventrolateral plates are densely crowded in specimens with empty stomachs, but become well spaced proximally when the specimens are expanded by a full stomach. The ventrolateral plates are still naked in the two small specimens from st. 30, with R/r 15/6 and 20/8 mm, but in all other specimens the ventrolateral area bears a varying number of granuliform spinelets, very scattered in some of the medium-sized specimens, but otherwise in a number of e. g. 6-7 in two tangential rows on each plate, or, as in a large specimen with R/r 128/18 mm, as many as about 20 granuliform spinelets in three tangential rows. Commonly the ventrolateral plates near the margin of the disk are more armed than the proximal ones.

Ventrolateral plates do not yet extend in the arms of the two small specimens from st. 30, R/r 15/6 and

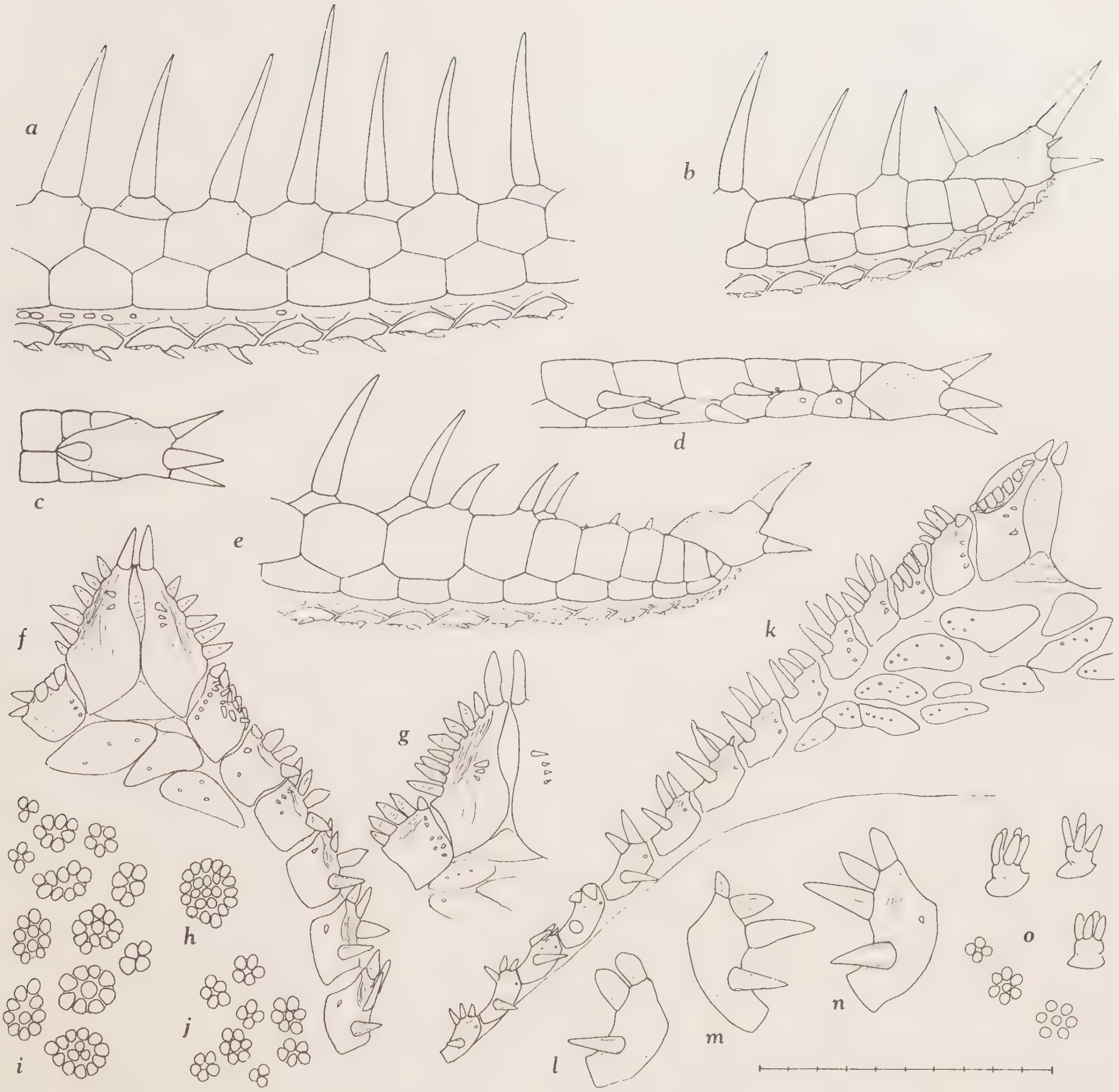
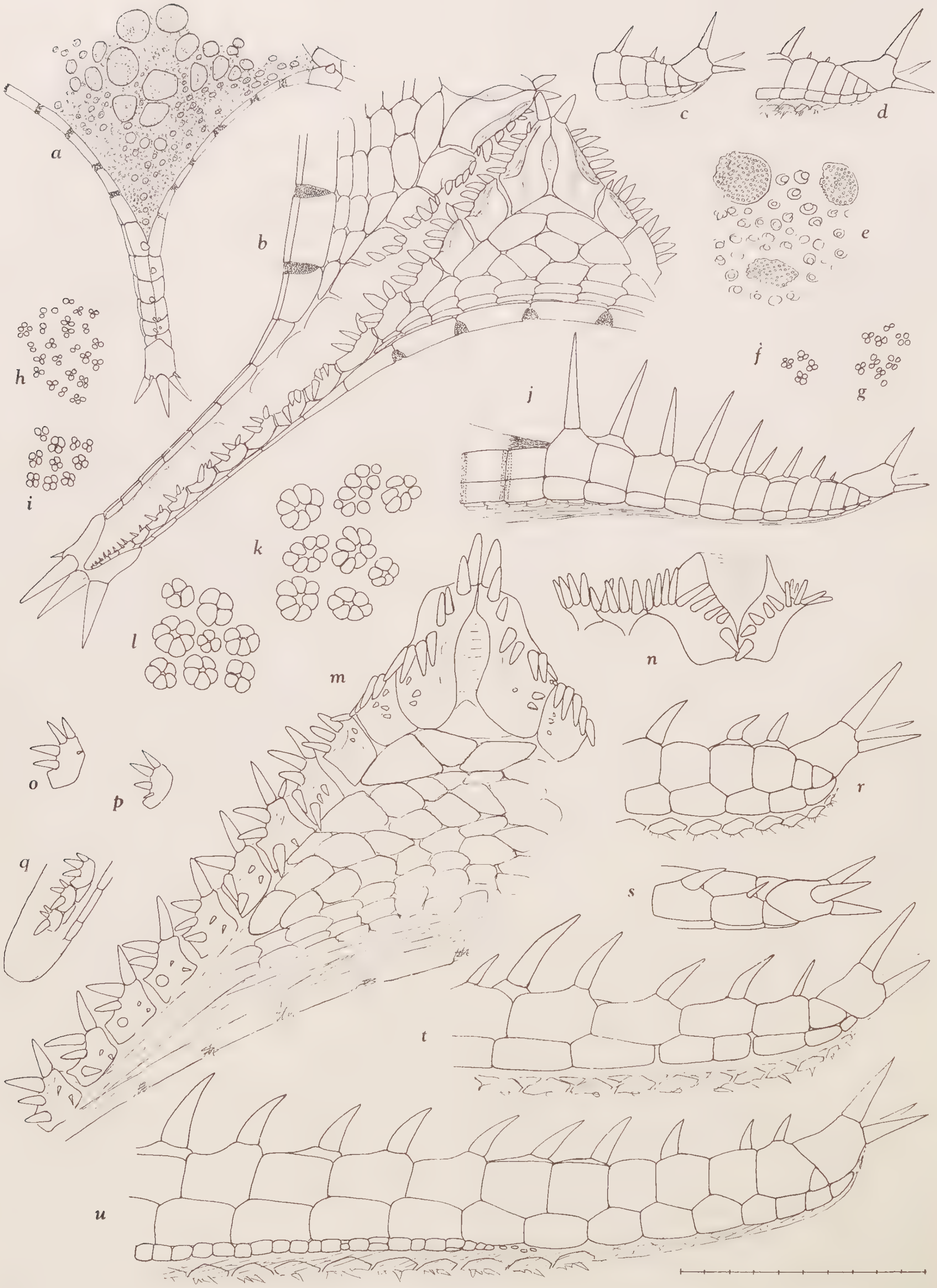


Fig. 16. *Styracaster horridus.* St. 663. a-e) R/r 72/15 mm, (see also k-o); a, part of arm showing the superomarginals nos. 11-18; b-c, distal end of same arm; d-e, another arm in dorsal view and in lateral view. f-j) R/r 74/16 mm; h-j, a large paxilla and two groups of paxillae, in four times the usual scale. k-o) R/r 72/15 mm; l-n, adambulacralia nos. 30, 17 and 15 respectively, in twice the usual scale; o, paxillae in four times the usual scale.
Scale: 10 mm (in l-n: 5 mm, in i-j, and o: 2.5 mm).

20/8 mm, but small rounded ventrolateral plates occur in the larger specimens in a narrow band rather far out in the arms, gradually becoming more and more scattered, so that in about the distal third of the arms there is only a narrow strip of naked skin between the marginal plates and the adambulacral and ambulacral ossicles. Only exceptionally, e. g. in the largest and perhaps senescent specimen with R 146 mm, ventrolateral plates occur also at the tip of the arms. Some of the ventrolateral plates in the arms of the large specimens may be provided with a few granules.

The specimens from the Kermadec Trench (figs. 16, 17; pls. VIII 3-6):

The two specimens of *Styracaster horridus* from st. 663 have R/r about 72/15 and 74/16 mm respectively. The material from st. 664 comprises a single large specimen with R/r 78/20 mm, a detached arm of a second equal-sized specimen, and five smaller specimens, of which one has R/r about 30/8 mm, whereas the others are juveniles with R/r 11/4, 14/5, 16/5, and 21/5 mm.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The adult specimens from the Kermadec Trench:

The number of superomarginals in these three large specimens is 20 in that with R/r 78/20 mm, 26 in that with R/r 74/16 mm, and 24 in that with R/r about 72/15 mm; and the opposite ones join from the sixth, the fifth, and the fourth pair, respectively.

The superomarginals of the arms are typically subquadrate to rectangular, and the accompanying inferomarginals are from three-fifths to less than half as high. In the same specimen there may be a considerable variation in the shape of the marginals in the different arms however, as will appear from the figures 17*t, u* of the distal part of two arms of the specimen with R/r 78/20 mm. In general the marginals are subalternating. The surface of the marginal plates is fairly granulated, especially in the specimen from st. 664. The superomarginals show a faint central depression. The arms may be very compressed.

These three specimens have an almost continuous row of dorsal spines on all arms. There are 18-19 spines on the arms preserved in their total length in the specimens from st. 663 with R about 72-74 mm, whereas the specimen from st. 664 with R/r 78/20 mm has 14, 15, 17, and 18 spines respectively on the four arms and 12 spines on the fifth arm which is in regeneration and only 53 mm long. The arm spines are subequal in length far out on the arms, and generally they are slightly curved towards the arm tip (fig. 16*a, b, e*). The first arm spine is typically developed on one of the plates of the first joining pair of superomarginals, but in one of the specimens from st. 663, it is in two of the arms developed on the plate just before the first one which joins its opposite. The proximal spines are about 6 mm long. Almost without exception the spines are placed with one to each pair of joining superomarginals. Some superomarginals may bear 2 spines, and a large spine may be accompanied by a couple of spinelets near its base.

The cribriform organs number 6-7 in the specimen with R/r about 72/15 mm, 7 in that with R/r about 74/16 mm, and 11 in that with R/r 78/20 mm. The structure is rather sublamelliform.

The terminal ossicles (dorsal to 1-4 superomarginals) carry generally 3 spines, a distal terminal one and a pair of smaller subterminal ones, but some terminal ossicles may have a fourth spine proximally in the dorsal midline (fig. 16*b*).

The whole dorsal area inclusive of the arm bases is provided with close-set paxillae. The number of spinelets in the paxillar crowns is on an average 4-6 in the specimen from st. 664 (fig. 17*l-k*), and 5-7 in that from st. 663 with R/r 72/15 mm (fig. 16*o*), but in both specimens paxillae occur with up to 9 spinelets. The second specimen from st. 663, with R/r 74/16 m, in general has paxillae with 9-12 spinelets (fig. 16*h, j*), but interspersed between these are also many with only 3 granuliform spinelets, and some with as many as 21 spinelets. Centrally on the disk the paxillae are small. None of the specimens show any indication of a central prominence. Neither papulae nor gonopores have been observed.

The adambulacral armature (fig. 16*f, k*) in these specimens is of the general type in *Styracaster,* not being modified as segmental papillae, and there is no distinct segmental pit developed.

The proximal 2-3 (4) adambulacral ossicles in the specimens from st. 663 carry 4, and some of the most proximal ones up to 6 flattened, but pointed furrow spines, the adoral one often smaller than the others. The following adambulacralia in these two specimens carry 4 and 3 furrow spines respectively. The aboral one, which is placed by itself on the narrow part of the ossicles, as usual slender conical and pointed, and the adoral ones of an about similar appearance. The most proximal adambulacralia in these specimens may carry, near their adoral margin, an irregular transverse series of up to 9 granuliform spinelets, and sometimes there are also a few granules on the medial or aboral part of the ossicles. The following adambulacralia within the disk area and in the proximal part of the arms, carry 1-2 subambulacral granules adorally, whereas the more distal ambulacralia have a naked surface.

In the specimen from st. 664 with R/r 78/20 mm (fig. 17*m*), the proximal two subrhomboid adambulacralia carry a uniform series of 4-5 furrow spines and adorally on their surface a small number

Fig. 17. *Styracaster horridus.* St. 664. a-b) R/r 14/5 mm; b, part of ventral side in twice the usual scale. c) R/r 16/5 mm. d) R/r 21/5 mm. e) R/r 16/5 mm, part of dorsal skeleton in four times the usual scale. f-g) R/r 21/5 mm (see also j), two groups of paxillae in four times the usual scale. h-i) R/r ab. 30/8 mm, two groups of paxillae in four times the usual scale. j) R/r 21/5 mm. k-q) R/r 78/20 mm (see also s-u); k-l, two groups of paxillae in four times the usual scale; o, p, q, adambulacralia nos. 20 26, and 32-34 respectively. r) Arm end of large specimen. s-u) R/r 78/20 mm; s-t, distal end of same arm in dorsal view and in lateral view; u, another arm in side view.
Scale: 10 mm (in b: 5 mm, in e-i, and k-l: 2.5 mm).

of subambulacral granuliform spinelets. The following few adambulacralia of the disk area bear adorally on their surface, in line with the one or two adoral subambulacral spinelets, a spine subequal to the furrow spines, and judging from the condition of the spine armature of the more distal adambulacralia, better considered as a distal furrow spine moved unto the subambulacral surface than as a real subambulacral spine. In the arms the adambulacral armature of 4 spines is positioned in the usual way, with all at the furrow margin, but the aboral spine is not larger, and perhaps even smaller than the adoral ones. The most distal adambulacralia, however, have not yet this aboral spine developed. In the present specimen with about 38 adambulacralia, those about no. 26 are the first with the aboral spine present, and not until the ossicles about nos. 20-18 does it reach a size as that found in the proximal part of the arms. An adoral subambulacral spinelet may be present on the ossicles far out in the arms.

The oral ossicles of the specimens from st. 663 (fig. 16*f, k*) are provided with from 6 to 9 marginal spines, the proximal one two or three times as long as the lateral ones, which are flattened and with a more or less pointed end. In one specimen there are oralia with 6, 7 and 9 marginal spines respectively. The oral spines are not modified as segmental papillae, and there is no distinct segmental pit. Both specimens bear on all oralia a fairly large suboral spine medially near the suture, and on some oralia there are a few additional suboral spinelets in a sutural row.

The oral ossicles in the specimen from st. 664 with R/r 78/20 mm (fig. 17*m*) bear 8-10 marginal spines, which are larger than is usually the case in the species, and although slightly flattened, rather terete. The proximal spine, about twice as large as the lateral ones, is placed a trifle higher on the ossicle (i. e. deeper in the mouth) than the others, the series of which extends below it almost to the suture. Each oral ossicle thus have two spines at its proximal end. Distally on their surface the oralia may bear up to 5 suboral spines. The primary oral ossicle shows the same, equilateral triangular ventral surface as in the Atlantic and Indian specimens.

The ventrolateral plates in the specimens from st. 663 are arranged in 7-10 tangential series and extend into the arms, reaching as far as to the marginals nos. 12-14. The ventrolateral plates of the disk area may carry up to about ten minute granules. In the specimen from st. 664, with R/r 78/20 mm, small ventrolateral plates extend in the arms as far as to the marginals no. 13. The ventrolateral area in this specimen appears to be devoid of granules.

The juvenile specimens from the Kermadec Trench:

The larger one of the remaining specimens of *Styracaster horridus* from st. 664, R/r about 30/8 mm and ≧ 30 superomarginals, has about the same characters as the full-grown specimens described. The superomarginal plates of the arms are rectangular, joining from plates no. 6. One arm, with the end lost, carries a continuous row of 8 dorsal spines, one to each pair of joining superomarginals. There are 7 cribriform organs in each interradius, and in one case an additional rudimentary one, yet consisting of only a single row of paxillae. The dorsal paxillae bear 3-4 spinelets. The number of furrow spines is 4-5 on the first adambulacral ossicle, 4 on the following ones, and 3 on those of the arms, all the furrow spines being straight and pointed. The oralia carry 6 marginal spines, flattened but all straight and pointed, not forming segmental papillae. The spine at the tip of the ossicle is as usual the largest. Ventrolateral plates occur in the arms at least as far as to the inferomarginals no. 8. The surface of the ventrolateral plates and of the oralia is naked, whereas there is a minute spinelet adorally on the surface of some of the adambulacralia in the arms.

The other four small specimens all show juvenile characters. They have R/r 11/4, 14/5, 16/5, and 21/5 mm, and 7-9, about 10, 11-12, and 14 superomarginal plates respectively, joining from plates no. 4 (or 5, in some arms of the smallest specimen). The number of arm spines is 2-4 in the specimen with R 11 mm, 3-4 in that with R 14 mm, 3-6 in that with R 16 mm, and 9 on the single intact arm of the specimen with R 21 mm. The cribriform organs number 3-5, 5-6, 7, and 5-7 respectively. The 3-5 cribriform organs in the specimen with R/r 11/4 mm are all still quite rudimentary, consisting only of a double row of papillae, one series to each side of the vertical marginal sutures. Similarly the outermost cribriform organs in the other specimens are only rudimentary. The terminal ossicles bear 3 spines in two of the specimens, and 5 spines in the two smallest ones, viz. a distal terminal one, a pair of slightly smaller subterminal ones, and dorsally on the ossicle a pair of very minute ones close to the unpaired terminal one. The first adambulacral ossicle carry 4-5 lanceolate furrow spines (5 in the smallest specimen), the following ones 3, and the most distal ones perhaps only 2 furrow spines. There is no subambulacral armature. The oral ossicles carry 6 (in some cases 7) lanceolate marginal spines, the proximal one the largest. A suboral armature is not developed except for a minute spinelet on one of the ossicles of the specimen with R/r about 16/5 mm. The ventrolateral plates, which are also naked, extend just into the proximal part of the free arms, in the specimen with R/r 21/5 mm e. g. to opposite the sixth inferomarginals.

The dorsal armature of these small specimens from st. 664 shows the gradual change from juvenile to adult state. In the specimen with R/r 11/4 mm there seems to be yet almost only the juvenile (embryonic) skeleton developed, consisting of the large embryonic (primary) plates and with smaller, supplementary (secondary) plates interspersed between them; only some very small plates, which probably are to be interpreted as the later paxillar shafts, are also present. The large embryonic plates are also still present in the specimen with R/r 14/5 mm, but further there are here numerous rudimentary paxillae, their number exceeding that of the small supplementary embryonic plates, many of them carrying a single granuliform spinelet, others yet consisting of the later paxillar shafts. In the specimen with R/r 16/5 mm the large embryonic plates are in absorbtion (fig. 17*e*), and the paxillae are still rudimentary and with only a single spinelet. In the specimen with R/r 21/5 mm the embryonic plates are entirely absorbed, and many paxillae have up to 4 spinelets, though all of them still very small (fig. 17*f, g*).

Concluding remarks: Ludwig considered the peculiar adambulacral and oral armature of his specimen a specific character. The same kind of armature, however, was actually found in the type-specimen of *Styracaster horridus*. The present material also shows that this characteristic appearance of the furrow armature, with the adoral spines modified as a kind of segmental organ, is of no definite importance in the specific diagnosis, since individual specimens may show the more usual porcellanasterid armature with spiniform instead of spatulate furrow spines. (The specimens at hand from the Kermadec Trench show the latter feature, besides transitional stages). It will appear from the following discussion of *Eremicaster* that segmental organs (papillae and pits) form an unstable character also in this genus.

The presence of ventrolateral plates in the arms, which was believed to distinguish *Chunaster* from *Styracaster*, is also an individually variable character (such as is also the possible presence of secondary dorsal arm plates in *Thoracaster*). In the juvenile specimens with R up to about 20 mm, ventrolateral plates may occur in the most proximal part of the free arms, as far as to the sixth inferomarginals, but they may also be entirely absent. In the large specimens ventrolateral plates usually occur in the proximal two-thirds of the arms, but may likewise be entirely absent, as in the two specimens available from the Galathea st. 282, and in Sladen's specimen. In some specimens, as e. g. the largest one available, R 146 mm, ventrolateral plates extend in the arms clear to the terminal ossicle. The ventrolateral skeleton in the arms may appear as a single series of fairly large subquadrate plates forming a regular pavement of the narrow area between the inferomarginal plates and the adambulacral and ambulacral ossicles, as e.g. in one of the arms of a large specimen from st. 664 (fig. 17*u*), or as a double series of relatively smaller rectangular plates, as in Ludwig's specimen, or there is one or more series of small oval or rounded plates, being gradually more and more spaced as they proceed outwards in the distal part of the arms (fig. 15*c-f*).

Biological remark:

Eggs, 0.5 mm in diameter, were found in the gonads of one of the larger specimens from st. 664.

Distribution:

Styracaster horridus is known hitherto from 15 dredgings: nine in the Eastern Atlantic, from the Bay of Biscay to the Gulf of Guinea; four in the northern Indian Ocean; and two in the South Pacific north of New Zealand (fig. 34). The known bathymetrical distribution is from 4040 to 5610 m. The kind of bottom on which it has been collected is sandy clay, calcareous clay, mud, muddy ooze, and globigerina or radiolarian ooze. The temperatures recorded range from 1.1° to 2.4°C.

Styracaster caroli Ludwig, 1907

Fig. 18. Pl. IX.

Styracaster sp. Ludwig, in Chun 1900 p. 449.
S. caroli n. sp., Ludwig 1907 p. 315.
S. caroli, Koehler 1909*a* pp. 43-45, pls. 3_5, 5_4.
S. caroli, Lieberkind 1932 pp. 281-282, text-fig. 8, pls. 4_{7-9}, 6_{9-11}.
S. horridus Wood-Mason & Alcock 1891*b*, p. 434; Alcock 1893 p. 86. (Non *S. horridus* Sladen).

Ludwig diagnosed this species on the basis of a single specimen collected by the Valdivia Expedition in the Indian Ocean, east of Zanzibar (st. 240: 6°12′S, 41°17′E, 2959 m, globigerina ooze, 2°C.). It has R/r 65/13 mm; 20 superomarginals; 14-16 dorsal arm spines, the proximal two of which are placed side by side in an oblique row; 7 cribriform organs; terminal ossicle with 3 spines. Closely crowded small paxillae with 3-4 granuliform spinelets; a low apical cone. Adambulacralia with 3 furrow spines; oralia with 6 marginal spines. Ventrolateral plates naked.

LIEBERKIND (1932) in the final report on the Valdivia porcellanasterids published some detail figures of the same specimen, but did not discuss it more closely and did not give any illustrations of its general appearance, finding this superfluous, since the specimen agreed well with those from the Investigator collections described in the meantime by KOEHLER. However, since it is useful to have photographs of type-specimens published, two photos from the archives of the Zoological Museum of Copenhagen are reproduced in figs. 1-2 pl. IX, showing the type-specimen of LUDWIG's *S. caroli* in ventral and in dorsal view respectively.

The three specimens of *S. caroli* which were described by KOEHLER in 1909 came from three dredgings of the Investigator in the Bay of Bengal (st. 117: 11°58′N, 88°52′E, 3197 m, globigerina ooze, 1.8°C.; st. 118: 12°20′N, 85°08′E, 3298 m, globigerina ooze, 1.7°C.; and in 6°18′N, 90°40′E, 2780 m). Those from stations 117 and 118 were previously recorded by WOOD-MASON & ALCOCK in 1891 (and ALCOCK 1893) but erroneously identified with SLADEN's *Styracaster horridus*.

The three Investigator specimens were apparently of about equal size. That from st. 118 has R/r 53/12$^1/_2$ mm; 20 superomarginals, longer than high, joining from plates nos. 4-5. A continuous series of dorsal arm spines (e. g. 12), the two larger proximal ones sometimes placed side by side as described for the type, but such an arrangement not always distinct. Seven cribriform organs. Terminal ossicle dorsal to two superomarginals, twice as long as broad, convex dorsally and with 3 short spines. Whole dorsal side with small paxillae with 3-4 granuliform spinelets. Adambulacral ossicles (32 in number) rectangular, proximal one with 4 conical pointed furrow spines, the adoral of which the longest, following ones with 3 furrow spines, the aboral of which isolated on the narrower part of the ossicle. No subambulacral armature except for an adoral granule on first to third ossicles. Oral ossicles with 7-8 marginal spines, lateral ones rather subequal to the furrow spines, proximal one larger; in general no suboral armature, only in one specimen 1-3 spines along the suture. Ventrolateral plates completely naked, arranged in about 5-6 tangential rows and further in radiating rows, not extending outside disk area.

WOOD-MASON & ALCOCK noted that specimens with the stomach empty show an apical cone, whereas none is seen when the stomach is distended. They record the colour in fresh state as "pale yellowish pink".

The Galathea material:

The species *Styracaster caroli* was collected in two dredgings in the Indian Ocean, north of Madagascar and in the Bay of Bengal respectively.

St. 234: 5°25′S, 47°09′E, 4820 m., 1.8°C. 2 specimens.
St. 314: 15°54′N, 90°17′E, 2600 m., 1.7°C., brownish ooze. 1 specimen.

The two specimens from st. 234 have R/r 93/about 24 (pl. IX 3-4) and 93-100/about 21 mm respectively. That from st. 314 has R/r 72/17 mm.

The number of superomarginals is 22 in the specimen with R about 72 mm, 26 in that with R 93 mm, and 27 in that with R up to 100 mm. The superomarginals join their opposites from plates nos. 5-6. The surface of the marginal plates is granulated. The proximal superomarginal plates of the arms are about one and a half time as long as high, and the inferomarginal plates are about half as high as the accompanying superomarginals. The superomarginals of either side of the arm may be almost regularly opposite each other, but usually they subalternate, and sometimes they are very regularly alternating, with the suture between them forming a zig-zag line (fig. 18*a*). Similarly the inferomarginals may correspond as well as alternate regularly with the superomarginals. As usual in the porcellanasterids the arrangement of the marginal plates may vary in the different arms of the same specimen. The larger dorsal arm spines are generally borne on distinct knobs on the plates.

The number of arm spines is 15 and 19 in the two intact arms of the specimen with R 72 mm, and 24-25 in the specimen with R 93 mm (pl. IX 5). The specimen with R 93-100 mm has 36 spines developed on one arm 95 mm long, and 22-27 spines on the other arms. In the specimens from st. 234 each of the plates of the first joining pairs of superomarginals bears a well developed spine (e. g. 8$^1/_2$ mm

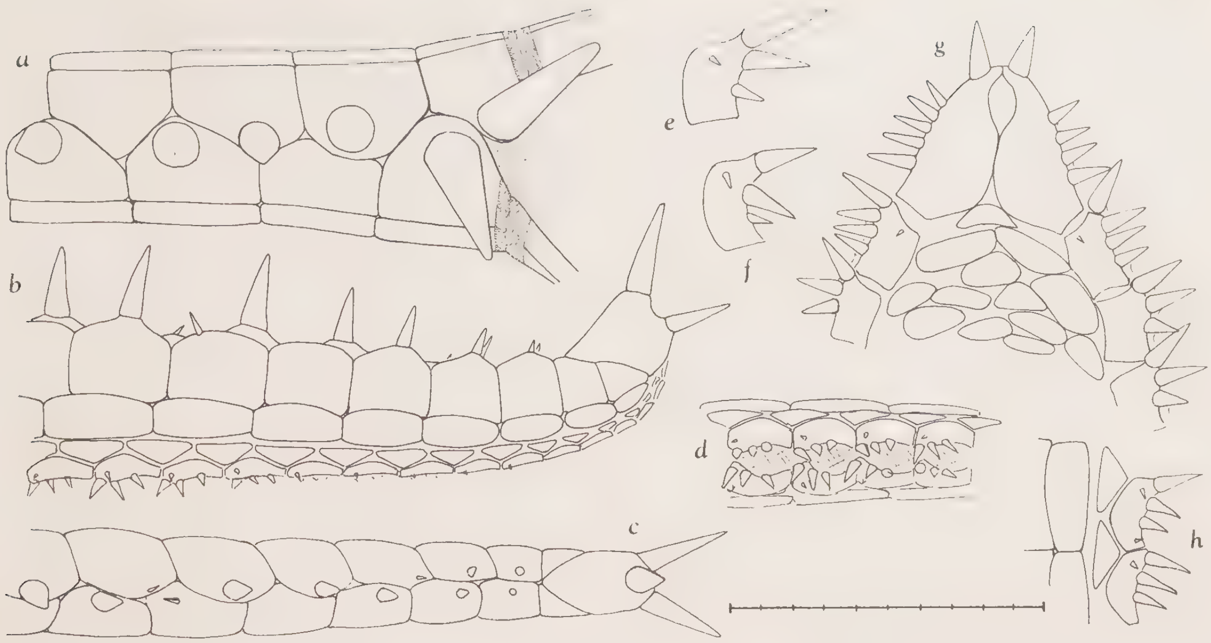

Fig. 18. *Styracaster caroli.* a-f) St. 234, R/r 93/ab.24 mm; b-c, distal end of arm in side view and in dorsal view; d, part of, same in ventral view; e-f, adambulacral ossicle no. 2, and one from the median part of the arm. g) St. 314, R/r 72/17 mm. h) St. 234, R/r 93-100/ab.21 mm, adambulacral ossicles from the median part of the arm, shown with their surface in the plane of the paper.
Scale: 10 mm.

long or almost as high as the arm), and at each arm base there are thus two subequal large spines somewhat displaced in relation to each other and widely diverging (fig. 18*a*). In the specimen from st. 314 there are two spines developed at one arm base (one spine to each of the plates in the first joining pair of superomarginals), whereas there is only a single spine at the two other arm bases. (The two remaining arm bases are torn away).

The arm spines are arranged in a straight continuous series in the midline for the whole, or at least the greater length of the arm, perhaps with only a single spine to each of the opposite pairs of superomarginals, but often with a spine on every plate in the then more or less regularly alternating series on either side of the arm. There may be a single series of arm spines clear to the terminal ossicle, but distally in some arms the yet rudimentary arm spines form a double row, a varying number of the distal superomarginals being opposite each other. Some superomarginals may bear two spines, but the additional one is generally only small. The arm spines decrease gradually and more or less regularly in length towards the end of the arms, and distally they are only rudimentary.

The cribriform organs number 9 in each interradius of the specimen with R/r 72/17 mm, 10-11 in the specimen with R/r 93-100/about 21 mm, and 11 in that with R/r 93/about 24 mm. The 9 median cribriform organs are well developed, whereas the possible additional ones are only rudimentary. The median cribriform organs comprise up to about 24 rows of papillae, and may almost touch their neighbours, leaving only a very narrow strip bare medially on the marginals.

The terminal ossicles are elongate, laterally compressed, dorsal to about two superomarginals, and provided with 3 spines, a moderately long distal terminal one, and a pair of slightly smaller subterminal ones (fig. 18*b*).

The whole dorsal area is covered with small paxillae with 3-4 short spinelets. The central area with smaller paxillae may be elevated into a faint apical cone. Papulae were not observable in any of the specimens. (Ludwig, in his diagnosis of the species, stated that papulae were not present.)

The madreporic body is subcircular, with the striae radiating from an adcentral point.

The adambulacral ossicles in the disk area are subrectangular, but in the arms they become subcrescentic and more elongate. The triangular ends of the ambulacral ossicles are in the arms very conspicuous between the series of adambulacralia and inferomarginalia. The first adambulacral ossicle carries 3 or, in the specimen from st. 314, 4 conical pointed furrow spines (fig. 18*g*). The following adambulacralia all carry 3 furrow spines, with two close together on the adoral part of the ossicle and the third smaller one medially on the ossicle, often a small distance from the adoral ones. The furrow spines of the disk area are larger than the proximal lateral oral spines. In the most distal part of the arms there may be only 2 adambulacral spines.

In the specimen from st. 314, with R 72 mm, a few of the proximal adambulacralia carry a minute subambulacral spinelet close to their adoral margin, whereas the other adambulacralia have a naked surface. In the two specimens from st. 234 with R 93 to 100 mm, nearly all the adambulacralia, almost to the tip of the arms, carry such an adoral subambulacral spinelet, and some of the proximal adambulacralia may bear two such spinelets (fig. 18*e, f, h*). In the specimen with R/r 93-100/about 21 mm, scattered adambulacralia may further bear a minute aboral subambulacral spinelet.

The oral ossicles (fig. 18*g*) are provided with 5-6 conical pointed marginal spines, the proximal one the largest; and the rather subequal lateral ones about half its size in the specimens from st. 234, but almost as long, though much more slender, in the specimen from st. 314. A suboral armature is not developed. The primary oral ossicle has a broadly triangular exposed surface.

The ventrolateral plates are transversely elongate, arranged in up to about 12 tangential rows in the specimen from st. 314, and in from about 10 up to about 15 indistinct tangential rows in the larger specimens from st. 234. Further they are arranged in more or less distinct radiating rows which correspond two and two with an adjoining marginal plate. They do not extend outside the disk area. The whole ventral area, including the ventral side of the arms, has been covered by a fairly thick integument, which, however, for the greater part has been rubbed off. The ventrolateral area appears completely devoid of granules or spinelets in the two specimens, but a few granules were found scattered in that with R 93-100 mm.

Remarks:

The present specimens of *Styracaster caroli* are somewhat larger than those hitherto known, and show correspondingly a larger number of cribriform organs and of dorsal arm spines. Otherwise they agree well with the type described by LUDWIG as well as with the specimens described by KOEHLER. It appears from the present material that the very characteristic doubling of the dorsal spines at the arm bases, found in the type from near Zanzibar and also in the two Galathea specimens from a more easterly locality, is not a reliable specific character, since it is not developed in some of the radii in the Galathea specimen from the Bay of Bengal, and was sometimes indistinct in KOEHLER's specimens from the Bay of Bengal.

Styracaster caroli in general appearance very much resembles *S. horridus*. It is distinguished from this species primarily by the character of the adambulacral armature.

Distribution:

Styracaster caroli is hitherto only known from the Indian Ocean (fig. 35), viz. from two dredgings in the area east of Zanzibar, and from four dredgings in the Bay of Bengal. It has been found in depths from 2600 to 4820 m, at temperatures of 1.7° to 2° C., and on a bottom of globigerina ooze and brownish ooze.

Styracaster elongatus Koehler, 1907
Fig. 19. Pl. X 1-2.

Styracaster elongatus n. sp., KOEHLER 1907*a* pp. 11-13, 1909*b* pp. 33-38, pls. $19_{5\text{-}6}$, $20_{2\text{-}4}$, $21_{3\text{-}5}$.
Styracaster elongatus, KOEHLER 1921 p. 2.
Styracaster horridus, RICHARD 1903 p. 66 (Non *S. horridus* Sladen).

KOEHLER described this species from a specimen with R/r ≧ 100/about 18 mm, dredged by the Princesse Alice in the Atlantic near the Azores (st. 1306: 37°17′N, 20°14′W, 4275 m, globigerina ooze). The specimen is mentioned previously in the literature, by RICHARD in 1903, but at that time erroneously considered a *Styracaster horridus,* and the station no., by a printers slip, given as 1036. KOEHLER in 1907, in his preliminary report on the Princesse Alice material, records also a second specimen, R/r ?/17 mm, from a neighbouring locality (st. 753: 39°52′N, 18°01′W, 4360 m, globigerina ooze), and in 1909, in the final illustrated edition of the report, he records still another specimen, R/r 55-60/13 mm, from a third locality in the same area (st. 527: 38°09′N, 23°17′W, 4020 m), besides an additional specimen, R/r ?/about 19 mm, from the station 753. (By a printers slip KOEHLER in 1909 gives the depth at st. 753 as 5360 instead of 4360 m). In 1921 KOEHLER finally records 3 specimens of *S. elongatus* from two Princesse Alice dredgings in the Bay of

Biscay (st. 2948: 46°46′N, 5°50′W, 3910 m, sandy mud; and st. 2986: 45°08′N, 7°06′W, 4870 m).

The type-specimen with R/r ≧ 100/about 18 mm, has 30-35 superomarginal plates, joining their opposites from no. 4. Marginals of disk slightly higher than long; superomarginals in arms slightly longer than high, inferomarginals somewhat lower. Up to a dozen conical pointed arm spines, confined to about the proximal two-third of arms. (In the type slightly curved away from the disk; but according to figures the reverse sometimes the case proximally in arms of other specimens). Seven cribriform organs. Terminal ossicle fairly conspicuous, with 3 spines. Closely crowded paxillae with 4-6 spinelets. A small apical cone. Adambulacralia with 5 fairly long furrow spines, and those of disk and proximal half of arms with 1-2 spinelets adorally and 1 small spine aborally on their surface. Oralia with a dozen marginal spines, the proximal of which by far the largest, and 2-3 suboral spinelets along sutural and 3-4 along distal margin. Ventrolateral plates in about 9 tangential rows, not extending outside disk area, and apparently naked. – In another large specimen from st. 753 they carry 1-3 small granules.

The specimen with R/r 55-60/13 mm has about 25 superomarginals, half a dozen arm spines (distal part of arms unarmed), and 5 cribriform organs. Adambulacralia with 4 furrow spines; proximal ossicles without subambulacral spines, but following ones with a single small spine aborally. No suboral armature. Ventrolateral plates apparently naked.

The Galathea material:

Specimens of *Styracaster elongatus* were collected in two localities in the Indian Ocean, in the Mozambique Channel, and south of Ceylon respectively.

St. 217: 14°20′S, 45°09′E, 3390 m, 1.6°C., globigerina ooze. 1 specimen.
St. 281: 3°38′N, 78°15′E, 3310 m, 1.8°C., globigerina ooze. 4 specimens.

R/r are in the specimen from st. 217 (pl. X 1-2) 74/18 mm, and in those from st. 281 about 55/14, 80/19, ≧ 80/21, and 81/23 mm.

The superomarginals number 23 in the specimen with R/r 55/14 mm, 26-27 in that with R/r 80/19 mm, and 27 in that with R/r 74/18 mm as well as in that with R/r 81/23 mm. The superomarginals join their opposites in the midline of the arm from plates nos. 5-6, or, in the specimen with R/r 80/19 mm, from nos. 4-5.

The superomarginals in the arms are subquadrate and the accompanying inferomarginals somewhat lower, being about one and a half times as long as high. All the marginals have a finely granulated surface, and their calcareous substance seems to be of a fairly porous structure. The superomarginals of either side of the arms may correspond as well as subalternate, and similarly the inferomarginals in the arms may sometimes alternate with the superomarginals to a varying degree.

The specimen from st. 217, with R 74 mm, has 4 dorsal spines on one arm, and 3 spines on the three other arms preserved. One of the larger specimens from st. 281, with R 80 mm, has 4 spines on two arms and 5 spines on the third arm left, whereas the specimen with R ≧ 80 mm has 2 spines on two of the arms and only a single spine on each of the other three arms, and the two remaining specimens, with R 81 and 55 mm, only a single spine to each of the five arms. There is always a spine at the arm base, placed on one of the plates of the first joining pair of superomarginals, and the possible additional spines are always found on plates of the more proximal part of the arms, so that the distal main part of the arms is unarmed. The first arm spine is always fairly robust, but not very long, its length being less than the height of the arm. It may be more or less distinctly curved towards the disk, whereas the other arm spines are straight and slightly curved against the arm end. The proximal arm spine in one of the large specimens is peculiar in having a broad flange on its distal side, which gives it a fan-shaped appearance.

The cribriform organs, which are of a papilliform structure, number 7-8 in the specimens with R/r 55/14 and 80/19 mm, the eighth additional one being rudimentary, 8-9 in the specimens with R/r 74/18 and 81/23 mm, and 9 in all the interradii of the specimen with R/r ≧ 80/21 mm.

The terminal ossicle (fig. 19*c, d, k*) is elongate, laterally compressed and with 3 spines, a terminal one about as long as the ossicle itself and a pair of somewhat smaller subterminal ones. The ossicle is dorsal to 2-4 superomarginals, and is most conspicuous in the smallest specimen, with R 55-60 mm.

The whole dorsal area, including the arm bases, is covered with close-set paxillae (fig. 19*e*). In the specimen from st. 217 the paxillae carry on an average 7-8 spinelets, but larger ones with up to 14 spinelets occur scatteredly. In the specimens from st. 281 the paxillae are generally smaller, with 4-7 spinelets, and the largest one observed in the differ-

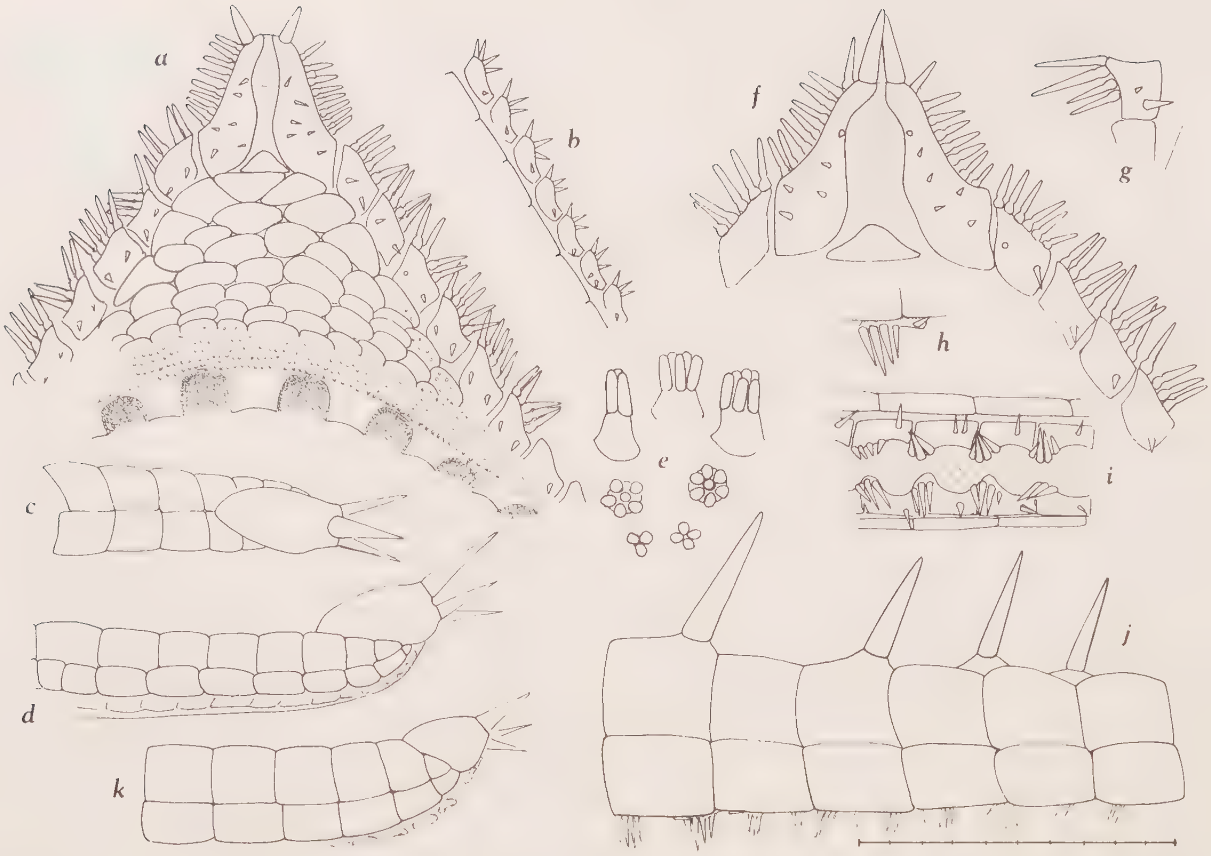

Fig. 19. *Styracaster elongatus*. St. 281. a-e) R/r 55/14 mm; a, part of ventral side (the figured interradius apparently shows the abnormal condition of having an odd marginal plate mid-interradially, instead of a suture. Another interradius shows the same feature, whereas the remaining three interradii in the specimen show the typical mid-interradial sutures); b, adambulacralia nos. 17-23, at the inferomarginals nos. 12-17; c-d, distal end of arm in dorsal view and in side view. f-j) R/r ≧ 80/21 mm; g, adambulacral ossicle no. 7; i, part of arm in ventral view, showing the inferomarginals nos. 8-10; h, one of the same adambulacralia figured with the furrow spines in the plane of the paper; j, proximal part of arm, showing the superomarginals nos. 8-13. k) R/r 81/23 mm.
Scale: 10 mm (in e: 2.5 mm).

ent specimens have 7, 8, 9, and 11 spinelets respectively. The central area of the disk, with smaller paxillae, may be elevated into a faint apical cone.

The madreporic body is circular, of a diameter about equal to the length of the adjoining marginals, and separated from these by a single row of paxillae. Its striae radiate from an adcentral point.

Papulae were observed in a small number on the outer half of the disk to each side of the mid-interradial line in a couple of the specimens from st. 281 which have the dorsal area well expanded by a full stomach. Their size is about twice that of the paxillar spinelets.

The proximal subrhomboid adambulacral ossicles (fig. 19*a, f*) carry a series of (4-)5, (exceptionally, in one arm of a large specimen, 6) subequal slender and generally rather terete furrow spines with a slightly enlarged basal part imbedded in a common web along the whole furrow. The adambulacralia of the arms generally have 3-4 furrow spines placed close together on the protruding adoral part. If there are 3 spines, the adoral one is often slightly larger than the others, if there are 4 spines, the second adoral one is often the largest (fig. 19*g*). On their surface the adambulacralia of the disk area, and sometimes those of the proximal part of the arms, carry two spinelets, a small adoral one and a larger aboral one. Exceptionally the first ossicle may carry 2 adoral spinelets, thus 3 subambulacral spinelets in all. In the main part of the arms only the aboral subambulacral spine is developed, possibly reduplicated on some ossicles, and most distally in the arms the surface of the ambulacralia is yet naked.

The oral ossicles (fig. 19*a, f*) of each pair forming a jaw are separated by a broad suture, and the primary oral ossicle is well exposed, showing a broad triangular ventral surface. Each oral ossicle carries 8 or 9 marginal spines, that at the proximal end much stouter and up to twice as long as the lateral ones, which are subequal, slender, fusiform, and slightly smaller than the proximal adambulacral spines. (One of the oralia in the specimen with R/r 80/19 mm is provided with two proximal spines, one above the other). Further the oralia carry a number of suboral spinelets, 2-4 along the suture, and also 2-4 near the distal margin.

The ventrolateral area is paved with comparatively small plates, in general transversely elongate, though not always so markedly as is usual in other species of *Styracaster,* and arranged in indistinct tangential and radiating series. Two radial series of ventrolateral plates may correspond in width with a marginal plate, but usually the number of plates is increased in the most distal tangential series so that 3 or 4 correspond with an adjoining marginal plate. The ventrolateral plates near the margin of the disk may be well provided with minute granules, and such may also occur scatteredly on the other plates. The main part of the ventrolateral area, however, usually appear naked, and this applies to the whole ventral area of one of the large specimens, but perhaps this is a matter of preservation, possible spinelets may be easily lost, and also the whole covering ventral integument is easily rubbed off.

The proximal ventrolateral plates are in general not markedly larger than the more distal ones, often only about twice their size, and though this is somewhat variable it appears to be a specific characteristic of the species. Ventrolateral plates do not extend outside the disk area.

The specimen with R/r 55/15 mm, st. 281, shows in three of the arm angles the normal mid-interradial suture, whereas to all appearance (cf. fig. 19*a*) there is in the two other arm angles a marginal plate in the interradial midline.

In general appearance *Styracaster elongatus* resembles *S. horridus* and *S. caroli.* It is best distinguished from these by the character of the adambulacral armature.

Distribution:

Styracaster elongatus is known at present from seven dredgings (fig. 35): five in the eastern North Atlantic, the Bay of Biscay and near the Azores; and two in the Indian Ocean, west of Madagascar and south of Ceylon. Its known bathymetrical distribution is from 3310 to 4870 m. The bottom on which it has been collected is globigerina ooze and sandy mud, and the recorded temperatures 1.8°C.

Styracaster chuni Ludwig, 1907

Figs. 3, 20. Pl. X 3-5

Styracaster sp., Ludwig, in Chun 1900 p. 491, fig.

S. chuni n. sp., Ludwig 1907 p. 314.

S. chuni, Lieberkind 1932 pp. 276-281, text-figs. 5-7, pls. $1_{3\text{-}4}$, $4_{2\text{-}6}$, $6_{12\text{-}15}$. 1935 pl. $5_{5\text{-}5\,a}$, 8.

S. chuni var. *groenlandica* n. var., Lieberkind 1935 pp. 26-29, text-figs. 9-10, pls. $1_{1\text{-}3,\,6}$, $3_{13\text{-}16}$, $4_{10\text{-}13}$, $5_{6\text{-}7}$.

Ludwig diagnosed this species on the basis of three specimens dredged by the Valdivia in the Atlantic, in the Gulf of Guinea (st. 63: 2°00′N, 8°04′E, 2492 m, 2.6°C.); and the same specimens were treated somewhat more exhaustively, and also figured, by Lieberkind in 1932. Lieberkind, in 1935, further described 12 specimens of *S. chuni* collected by the Ingolf in the southern part of Davis Strait (st. 37: 60°17′N, 54°05′W, 3229 m, 1.4°C.), which specimens he, however, considered represented a new variety.

The three Valdivia specimens (the type-material) have R/r ranging from 41/14 mm over R 44 mm to 57/19 mm; 12-14 subquadrate superomarginals, joining from plates no. 5; inferomarginals only half as high as long, all marginals with a finely granulated surface; 2-5 large pointed arm spines; 5-7 cribriform organs. Terminal ossicle elongate, laterally compressed, with 3 spines, a large distal one and a pair of smaller subterminal ones. Dorsal paxillae uniform, small, close-set, with 4-6 (-8) spinelets, not present in arm bases, however, where there is a pavement of naked plates. No distinct apical cone. Madreporic body round, with striae radiating from adcentral margin. Adambulacralia with a curved furrow margin, with 3 (sometimes 2 and proximally perhaps 4) pointed furrow spines, and with 1-2 (3) subambulacral spines, viz. an aboral one, generally fairly large and only in rare cases absent, and on the more proximal ossicles usually one or two adoral ones. Oralia with 4-6 marginal spines, proximal one twice as large as lateral ones, and a few suboral spinelets near sutural or distal margin. Ventrolateral plates naked, arranged in 6-9 tangential rows, not extending outside disk area. Ventral area covered by a thick integument.

Of the twelve Ingolf specimens recorded by Lieberkind (1935), one has R 52 mm, 15 superomarginal plates, and 7 cribriform organs; another of about the same size has only 5 cribriform organs in each interradius, but one with R only 24 mm has also 7 cribriform organs developed, though the outermost ones rudimentary. The number of dorsal spines on each arm varies from 1 to 6.

Lieberkind described these specimens as representing a new variety, var. *groenlandica,* which he considered distinguished from the typical form by having smooth, or almost smooth marginal plates, and by having higher paxillar shafts and more slender paxillar spinelets. The specimen on which Lieberkind seems to have based his description of the variety, R 52 mm (pl. 1, 1), is well distinguished by these characters from the specimens from the Gulf of Guinea, which the present author was able to ascertain by a re-examination, but others of the Ingolf specimens are rather intermediate. Lieberkind also wrote: "Whether the variety can be upheld later, when a greater material from more localities are collected, is difficult to decide now, the more so as the characters of the species seem to be rather inconstant." As a further justification for the erection of the variety *groenlandica,* Lieberkind refers to the "wide separation" of the two localities, the Gulf of Guinea and the Davis Strait. – With regard to the fauna of the ocean bed below 2500 m, these two localities, however, are really not widely separated.

The Galathea material:

Specimens referable to *Styracaster chuni* were collected in four dredgings, two in the eastern tropical Atlantic, near the type-locality and off Angola respectively, and two in the South Pacific, in the Kermadec Trench north of New Zealand.

St. 52: 1°42′N, 7°51′W, 2550 m, muddy clay. ca. 3°C. 6 specimens.
St. 99: 8°40′S, 11°10′E, 2690 m, yellowish clay, 3.9°C. 7 specimens.
St. 663: 36°31′S, 178°38′W, 4410 m, 1.2°C., brown, sandy clay. 2 specimens.
St. 664: 36°34′S, 178°57′W, 4510-4570 m, 1.1°C., brown sandy clay. 5 specimens.

The Atlantic material (figs. 3, 20*a-h*):

The present Atlantic specimens of *Styracaster chuni* are all fairly large ones. Those from st. 52 have R/r 39/12, 41/14, 43/14, 44/13, 44/14, and 49/15 mm respectively, and three of those from st. 99 have R/r 56/18, 60/19, and 64/21 mm respectively. (The remaining four specimens from st. 99 are of about the same size, but have to be left out of consideration, since they are present in the form of loose skeletons only, probably having been dried without previous preservation).

The number of superomarginals in these specimens are 11-12, 12-13, 13-14, 12-13, 12-13, 15, 13-14, 17-19 (by R 60 mm), and 14 (by R 64 mm). The joining of the opposite superomarginals of either side of the arms takes place at the fourth, fifth or sixth plates, varying independently of the size of the specimens. The superomarginals of the arms are subquadrate, and usually they stand opposite each others, but any degree of alternation may be found in their arrangement, and similarly the inferomarginals of the arms may alternate to a varying degree with the superomarginals. The inferomarginals in the arms are about half as high as the accompanying superomarginals. All the marginals are rather granulated.

The number of dorsal spines to each arm is usually 2 or 3, but there may be as many as 6 spines. One of the specimens from st. 52, with R/r 44/13 mm, has only a single dorsal spine on each arm, while another from the same population, R/r 49/15 mm, has 6 spines on two arms and 5 spines on the three other arms. There is always a spine developed on one of the plates of the first pair of joining superomarginals, and the other spines – if such are present – are usually placed on the proximal half of the arms, but they may also be found scattered along the whole length of the arms. Normally, only one of the plates in each joining pair of opposites bears a spine, and the spines may then be developed on succeeding pairs of superomarginals, on plates of the same side of the arm, or alternatingly on plates of either side, or the spines may be scattered along the arm, with one or more pairs of naked plates in between. Occasionally both plates in a joining pair of opposites have a spine developed, and these spines are then generally of unequal size, but e. g. the specimen with 5-6 arm spines has proximally on two arms 2 large subequal spines side by side, one to each plate of the first joining pair of superomarginals. Rarely a single superomarginal plate may carry 2 or 3 spines, a large one and 1-2 additional small ones. The dorsal arm spines are fairly robust, conical, pointed, up to about twice as long as the superomarginal plates on which they are borne, and usually slightly curved towards the disk. The proximal spine is the largest, but the other spines of the arms are usually almost just as large. The spine-bearing plates are somewhat enlarged and dorsally protruded so that a conical base for the spine is formed.

The cribriform organs are present in a number of 7 in each interradius in four of the available nine specimens. Two specimens, R/r 39/12 and 44/13 mm, have only 5 cribriform organs, two others, R/r 56/18 and 64/21 mm, show also only 5 well-developed cribriform organs in each interradius, but, in addition, there may be 1-2 rudimentary ones; and one specimen with R/r 49/15 mm has 9 cribriform organs in each interradius, viz. a series of 7 well-developed ones and a rudimentary one to each side. (The smallest specimen of *Styracaster chuni* which the present author has examined, one from the Ingolf st. 37 with R 19 mm, but not mentioned by LIEBERKIND, had already 7 cribriform organs developed in each interradius).

The number of cribriform organs is individually variable and not merely connected with the age of the specimens, though specimens which originally had 5 or 7 cribriform organs (apparently developed almost simultaneously in the juveniles) with growth may add an additional cribriform organ to one or to both sides of the original series. The cribriform organ is usually of a distinctly papilliform (or better spiniform) structure, but occasionally a cribriform organ may appear rather lamelliform, the papillae being flattened in the vertical plane and fairly broad. The structure of the cribriform organ is thus a taxonomical character which should be used with some caution. Dorsally the cribriform organs are only imperceptibly demarcated from the paxillated disk, whereas they are well marked off ventrally, the series of covering papillae extending from one lateral dorsal corner of the organ downwards almost to the ventral edge of the inferomarginal plate, here bending and continuing close to the margin across the vertical marginal suture to the other side of the organ, and up to its other lateral dorsal corner. Usually the cribriform organs are bordered by straight parallel sides and well separated from each other; their width (number of series of papillae up to about 20) increases with age however, and in some specimens some of the median cribriform organs join their neighbours dorsally and ventrally, leaving free only a narrow streak on the marginals. The outermost rudimentary organs may occasionally be developed either on the superomarginal plates alone or on the inferomarginal plates alone.

The terminal ossicle (fig. 20*h*) is fairly conspicuous. It is distal to the arm end, dorsal to only one rudimentary superomarginal plate, and about as large as the two distal superomarginals together. Typically it is provided with three spines, a very conspicuous large distal terminal one, its length usually exceeding that of the ossicle itself, and a pair of much smaller subterminal ones. Two large distal spines, placed side by side, is found as an abnormality in a single arm, and sometimes there are two pairs of small subterminal spinelets. The large terminal spine constitutes a conspicuous character in the species.

Dorsally, on the main part of the disk, there is a close covering of small paxillae, crowned with 3-7 spinelets, (in different specimens e. g. 3-4, 4-5, or 3-6 paxillar spinelets), and paxillae with as many as 10 spinelets occur scatteredly in some specimens. The paxillae are subequal in height, the shaft in the larger ones about as wide as high, and in the smaller ones about half as wide as high. Centrally on the disk the paxillae are small, and a distinct, though small, apical cone is present in some specimens. At the arm bases, between the marginal plates, there is always a small area without paxillae, but with a pavement of fairly large naked plates, and apparently this is an important specific character. The proximal arm spines, however, may sometimes be placed in such a way that this area with plates becomes rather obscured.

The madreporite is roundish and of a diameter about the length of the superomarginals, quite close to these or separated from them by one or a few series of paxillae. Sometimes the median pair of superomarginals in the interradius with the madreporite is lower than the others, making room for the madreporite which then becomes in part marginal in position. The striae all radiate from an adcentral point, or some of them stretch across in radial direction.

Papulae have not been observed. The gonopores were traced in a specimen from the Ingolf Expedition as a minute papilla at a distance of a single series of paxillae from each of the sutures between the first and second superomarginal plates.

The most proximal adambulacral ossicles are subrhomboid (fig. 20*a*), but in the following ones the furrow margin becomes excavated to give room for the podia, and in the arms the aboral part of the adambulacralia becomes distinctly narrower than the adoral part. The proximal adambulacralia bear on their furrow margin a series of 3, sometimes 4, exceptionally even 5, conical pointed subequal spines. The more distal adambulacralia have 2-3 (perhaps most commonly 2) widely diverging furrow spines placed either close together on the adoral broader part of the ossicle or with the aboral one placed medially on the furrow margin at some distance from the adoral one(s) (fig. 20*b*, *c*). Scattered adambulacralia may have 1-2 additional spinelets aborally on the furrow margin of the narrow part of the ossicle (fig. 20*g*). The whole series of furrow spines is joined by a distinct web.

On their surface the adambulacralia bear usually 1-2 (fig. 20*b, c*), but exceptionally 3-4 spinelets or spines, e.g. on some of the more proximal adambulacralia in disk and arms of some of the large specimens (fig. 20*d-f*). If 4 subambulacral spinelets or spines occur, they may be placed two and two side by side near the adoral and aboral margins respectively, but they may also be more irregularly distributed. If there are 2 subambulacral spinelets or spines they are placed with one near the adoral margin, and one at the interradial aboral corner respectively. The aboral subambulacral spinelet or spine seems characteristic of the species. It is usually a well developed spine, and it is absent only in very rare cases.

The ambulacral furrow can be almost completely closed by the ambulacral ossicles meeting over it, but can also be widely opened, and in this case the arms appear as constricted at their bases.

The oral ossicles bear 5-7 spiniform or conical, and sometimes slightly flattened marginal spines, the proximal of which is two or three times as large as the others, and further a number of suboral spinelets, varying from 1 or 2 fairly large ones near the distal margin, or near the suture, to 7 placed in a row along the distal and sutural margin, or more rarely scattered irregularly over the whole surface of the ossicle.

The primary oral ossicle is fairly broad and usually very conspicuous. In the arms the triangular ends of the ambulacral ossicles are distinctly seen wedged in dorsally between the adambulacralia (fig. 3*p*).

The ventrolateral plates are naked in all the specimens. They are transversely elongate, the proximal ones in general much larger than the distal ones, and arranged in tangential and in usually indistinct radial series. The number of plates in the proximal tangential row varies from 1 to 6. Two radial series of plates may correspond with a marginal plate, but the number of distal plates corresponding with a marginal one may also be 3 or 4.

A thick integument covers the ventral and also the dorsal side in several specimens.

The Pacific material (fig. 20*i-p*. Pl. X 3-5):

The seven specimens of *Styracaster chuni* available from two dredgings in the Kermadec Trench have R/r 36/12, 38/13, 50/17, 51/18, 54/14, and 55/17 mm. The two largest specimens are from st. 663, the other four from st. 664, and further from this station there is a fifth, fragmentary specimen of the same size-group. The ratio R/r ranges from a little less than 3 to almost 4 (this latter, however, in a specimen with an empty stomach, and with the disk markedly excave interradially).

The superomarginal plates number 17, 15, 18, 15, 18, and 17 respectively, and join their opposites from plates nos. 4-6. The superomarginals are subquadrate, and the inferomarginals in the arms are about half as high as their superomarginal companions. In the arms the superomarginals are exactly opposite each other or alternate more or less regularly, as described for the Atlantic material, and they may then be pentagonal in shape, even hexagonal if also alternating with the adjoining inferomarginals. The surface of the marginal plates is rather smooth as was the case with the specimens from the Davis Strait described by LIEBERKIND.

The number of arm spines in these specimens varies in the same way as it did in the Atlantic ones. The two larger specimens (st. 663) have 3-4 dorsal spines on each arm (only on a single arm 2); the specimen with R/r 50/17 mm has 4-5 arm spines, that with R/r 36/12 mm has 2-3 arm spines, whereas the other three specimens from st. 664 have only 1-2 spines on each arm, one of them even only a single spine on four of the arms. In two of the specimens with only 1-2 arm spines (R/r 38/13 and 51/18 mm) the proximal (and perhaps only) spine is placed not on one of the plates of the first pair of joining superomarginals, as is the case in all other specimens of *Styracaster chuni* known, but on plates of the second and the third joining pairs respectively. The superomarginal plates in these specimens join their opposites from nos. 5 and 4 respectively, and it is always the sixth plate which bears the most proximal spine. The arm spines in the specimens from the Kermadec Trench on the average appear slightly smaller and more slender than those in the Atlantic specimens known. They are likewise curved slightly in the direction towards the disk.

The cribriform organs are present in a number of 5 to each interradius in three specimens with R/r 38/13, 51/18, and 54/17 mm; in the others they number 6-7, but the additional organs to one or to either sides of the 5 median ones are usually rudimentary. The structure of the cribriform organs is papilliform or rather sublamelliform, the papillae being dis-

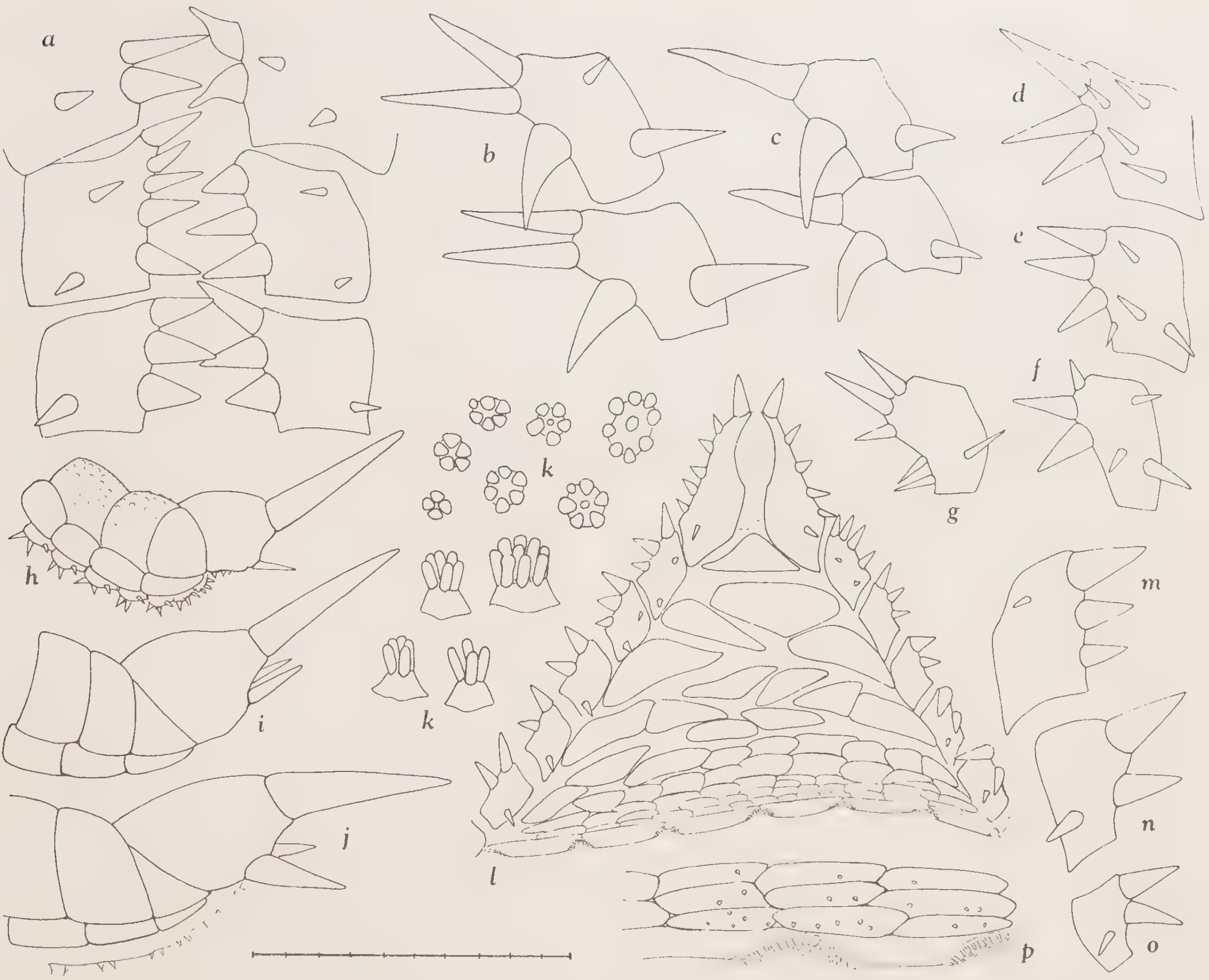

Fig. 20. *Styracaster chuni.* a-c) St. 99, medium-sized specimen, R ab. 60 mm; a, distal part of oral ossicles and adambulacralia nos. 1-2; b-c, adambulacralia nos. 6-7 and 10-11 respectively. d-f) St. 99, another medium-sized specimen, R ab. 60 mm, adambulacralia nos. 5, 10, and 14 respectively. g) St. 99, a third medium-sized specimen, R ab. 60 mm, adambulacral ossicle no. 17. h) St. 99, R/r 60/19 mm, the granulated surface is indicated on some of the marginalia. i) St. 664, R/r 36/12 mm. j) St. 663, R/r 55/19 mm. k-o) St. 664, R/r 50/17 mm; m,n,o, adambulacralia nos. 1 and 5, and one from the median part of the arm. p) St. 664, R/r 51/18 mm, part of ventral area mid-interradially.
Scale in 1: 10 mm, in a-j and m-p: 5 mm, in k: 2.5 mm.

tinctly flattened in the vertical plane. In one specimen the supero- and inferomarginal plates in some of the interradii do not quite correspond with each other, which results in some irregularity in the arrangement of the cribriform organs.

The terminal ossicles are, as is characteristic also of the Atlantic specimens, fairly conspicuous, with a large distal terminal spine and a pair of usually much smaller subterminal ones (fig. 20*i, j*).

The paxillae, covering the main part of the disk, carry generally 4-7, but occasionally 8 or 9 spinelets (fig. 20*k*). The paxillar shafts are about as wide as high, and the spinelets are about as long as the height of the shafts. The central area with crowded small paxillae, is slightly elevated in some specimens. At the arm bases, for an area corresponding to about two marginal plates, no paxillae are developed, and instead there is a pavement of plates of a somewhat varying size (pl. X 5), but distinctly larger than the paxillar bases, and sometimes so crowded that they partly cover each other. As noted in the description of the Atlantic specimens, this pavement of plates in the arm bases seems an important specific character.

The madreporic body is circular, close to the marginals or separated from these by two rows of paxillae. The striae may stretch across in radial direction or may all radiate from an adcentral point.

The more proximal adambulacral ossicles of the disk area are provided with a furrow series of 3-4 spines and bear normally 1-2 adorally placed granules or spinelets on their surface and an aborally placed spinelet (fig. 20*l*). Some ossicles among the first 1-3, may have only the aborally placed subambulacral spinelet developed (fig. 20*m*), and even this may be missing, and the surface of the more proximal adambulacralia completely naked. The more distal adambulacral ossicles have usually only 2 furrow spines, conical, pointed, and placed on the adoral broad part of the ossicle, and invariably a small aborally placed subambulacral spine (fig. 20*n, o*). As mentioned in the discussion of the Atlantic specimens, this aboral subambulacral spine (only sometimes absent on the more proximal adambulacralia) seems to constitute a constant specific character.

The oral ossicles carry 4-6 marginal spines, the proximal of which more or less distinctly larger than the others. Their surface is naked or maybe provided with 1 (-2) spinelets distally (fig. 20*l*).

The ventrolateral plates (fig. 20*l, p*) are arranged in about 7-10 tangential rows. Distally they are small, transversely elongate and closely crowded, overlapping each other, proximally they are larger, often also transversely elongate, but sometimes of any other possible shapes. Often there is only one plate in the first tangential row and only two plates in the second row. The ventrolateral plates are further typically arranged in distinct radial series which correspond two and two with the adjoining marginal plates; but their number may be increased distally in some interradii in which then 3 or maybe 4 plates adjoin each marginal one. The ventrolateral plates in general appear naked as was also the case in all examined Atlantic specimens of *S. chuni*. Two specimens, however, with R/r 38/13 and 51/18 mm, have up to half a dozen granuliform spinelets on the most distal ventrolateral plates (fig. 20*p*), and 1-2 granuliform spinelets on some of the other plates. Also another specimen has single granules on a few of the more proximal plates.

Remarks:

There can be no doubt that these Pacific specimens belong to the species *Styracaster chuni,* hitherto known only from the Atlantic. Their marginal plates appear somewhat more smooth than do those in the specimens from the Gulf of Guinea; but in this respect they are similar to specimens from the Davis Strait. A few of the Pacific specimens examined, have a modestly developed ventrolateral armature of granuliform spinelets, whereas all Atlantic specimens examined, had a naked ventral side. This latter feature, however, applies also to other of the Pacific specimens, and the possession of ventrolateral granules or spinelets thus cannot be considered of any decisive taxonomic importance. In all other characters, the Atlantic and the Pacific specimens examined show an identical variation.

Distribution:

Styracaster chuni is known from six dredgings (fig. 36): four in the Atlantic, in the Davis Strait and the area of the Gulf of Guinea, and two in the South Pacific, in the Kermadec Trench north of New Zealand. Its bathymetrical distribution is from 2550 to 4510-4570 m. It is found at temperatures from 1.1° to 3.9° C. The bottom recorded always is clay. It is a fairly robust species and perhaps there is a connection between its robust appearance and its occurrence on a clay bottom.

Styracaster paucispinus Ludwig, 1907

Ludwig 1907 pp. 315-316.
H. L. Clark 1920 pp. 80-81, pl. 2_{3-4}.

This species was preliminarily described by Ludwig from two specimens collected by the Albatross in the eastern tropical Pacific (st. 4658: 8°30'S, 85°36'W, 4335 m, fine green mud, 1.8° C.). The same material was briefly discussed in 1920 by H. L. Clark, who also published photographs of one of the specimens in dorsal as well as in ventral aspect.

The two specimens have R/r 19/9 and 22/9 mm; 6 and 7 superomarginals (according to the photo joining from no. 5); 1-2 (3?) arm spines; 3 broad cribriform organs; terminal ossicle with 3 spines. Dorsal side with closely crowded small paxillae with 4 (-6-8) spinelets (according to the photo confined to main disk area, whereas there is a pavement of naked plates in arm bases). A small apical cone. (The madreporic body in the photographed specimen roundish, with striae radiating from proximal margin). Adambulacralia, 12-13 in number, with 5 blunt furrow spines (having the appearance of segmental papillae and covering a distinct segmental pit, - according to the photo and to Clark's reference to a "marked depression or shallow furrow on the ventral surface ... from the inner adoral corner of the plates, where it is deepest, to the outer aboral corner, where it flattens out entirely"). No subambulacral armature. Oralia with 7 marginal spines, proximal one the largest, and a suboral spinelet near the suture. Ventrolateral plates with spaced granuliform spinelets (according to Clark, however, apparently wanting in one of the specimens).

LUDWIG did not discuss the possible relationships of his *S. paucispinus,* but H. L. CLARK made some considerations thereupon, comparing the species to *armatus, spinosus,* and *edwardsi,* on account of their number of cribriform organs, but noting that it differs from these in the shortness of the arms and correspondingly small number of arm spines. (LUDWIG gave the number of arm spines as 2-3, which, however, would hardly agree with the number of superomarginals stated, and H. L. CLARK also found only 1-2 arm spines, when he re-examined the specimens. But in counting the superomarginals LUDWIG may have neglected possible rudimentary ones below the terminal ossicle).

An important character, missed by both LUDWIG and CLARK, is the armature of naked plates at the arm bases, which appears from the photo. This characteristic, combined with an armature of fairly well developed paxillae on the main part of the disk, these two specimens share only with LUDWIG's *Styracaster chuni.* The ratio R/r, and furthei the low number of cribriform organs and the paucispine condition of the arms, agree also well with young equal-sized specimens of *S. chuni.* What distinguishes *S. paucispinus* from *S. chuni* is primarily the appearance of the adambulacral armature, with the furrow spines modified as segmental papillae over a distinct segmental pit. Propably, however, this may not be a constant character (considering the variability of the adambulacral armature in *S. horridus* and *Eremicaster crassus* e. g.), and in that case a distinguishing character may perhaps be found in the presence of an aboral subambulacral spinelet in *S. chuni,* whereas in *S. paucispinus* the aboral subambulacral surface appears to be naked.

The two specimens known of *S. paucispinus* are possibly young ones (if the size reached by other species of *Styracaster* is considered), and though they apparently have attained the adult characters, at least in the main, larger specimens, besides a larger number of arm spines and perhaps of cribriform organs, may show a better developed suboral armature and perhaps also have a subambulacral armature on the more proximal ossicles.

Styracaster robustus Koehler, 1908

KOEHLER 1907*b* p. 144 (nom. nud.), 1908 pp. 560-561 (224-225), pl. $4_{44\text{-}45}$.
WILTON 1908 pl. 13 fig. 39.

KOEHLER described this species on the basis of a single specimen collected by the Scotia Expedition in the Atlantic sector of the Antarctic (51°07'S, 9°31'W, 3846 m, diatom ooze). It has R/r 45/15 mm; 17 superomarginal plates, all higher than long, joining from plates no. 7; 2 conical pointed arm spines, on 7th and 9th pair of superomarginals, the larger proximal one slightly curved towards the disk; inferomarginals of arms apparently about half as high as superomarginals; 11 cribriform organs; terminal ossicle fairly inconspicuous, with a large distal terminal spine and a pair of smaller subterminal ones. Dorsal side (including arm bases, according to the photographs published by WILTON) with numerous close-set paxillae with 3-4 (5) granuliform spinelets. A conspicuous round madreporite. Adambulacralia with 4-5 furrow spines and some granules on their surface. Oralia with 8-9 marginal spines, proximal two, especially the first, enlarged, the others subequal to the adambulacral spines, and with several irregular rows of suboral granules. Ventrolateral area covered with a thick integument with granules.

The type-specimen of *S. robustus* evidently has an empty stomach, and the interradii consequently unusually excave, and probably the radius of the disk would be half the arm length if the stomach was full. The species may be grouped together with *S. chuni* and *S. paucispinus,* which have also relatively short arms. It is easily distinguished from these, however, by the uniform covering with paxillae over the whole dorsal area inclusive of the arm bases, and also by its different oral and adambulacral armature.

Styracaster armatus Sladen, 1883

Fig. 21

SLADEN 1883 pp. 232-234; 1889 pp. 153-154, pls. $24_{1\text{-}4}$, $28_{1\text{-}4}$.
WOOD-MASON & ALCOCK 1891*b* p. 434; ALCOCK 1893 p. 86.

SLADEN described this species on the basis of a single specimen dredged by the Challenger in the mid-Pacific near the Caroline Islands (st. 224: 7°45'N, 144°20'E, 3384 m, globigerina ooze, 1.9°C.). WOOD-MASON & ALCOCK have later recorded the species as taken by the Investigator in two dredgings in the Bay of Bengal, in depths of 3365 and 3519 m respectively, and on a bottom of globigerina ooze.

The type-specimen has R/r 38/11 mm; 9 superomarginals, considerably longer than high, joining from plates no. 4; a continuous row of 5 arm spines;

inferomarginals lower than superomarginals, about three times as long as high; 3 broad papilliform cribriform organs. Terminal ossicle fairly inconspicuous, with 3 spines. Dorsal side with a thick integument with closely crowded minute imperfect pseudopaxillae and simple spinelets, and with naked spaces at arm bases. A faint apical cone. (Madreporic body according to figure round and with striae radiating from its center). Adambulacralia elongate (vertebra-shaped), with 3 pointed slightly compressed furrow spines on adoral half, and a single small conical subambulacral spine near interradial adoral corner. Oralia large, markedly coulter-shaped, only joining their opposites proximally, being widely separated also medially, where the primary oral ossicle is well exposed; each oralia with 5-6 marginal spines, proximal one not much larger than lateral ones, and with a few spinelets on distal surface. Ventrolateral area with naked squamous plates arranged in tangential and radiating series.

The Galathea specimen:

St. 280: 1°56′N, 77°05′W, 4350 m, 1.3°C., globigerina ooze. 1 specimen.

This specimen, taken S. W. of Ceylon, agrees well with the type-specimen described by SLADEN, showing only negligible variations in some characters. It has R/r 39/13 mm, and is thus of about the same size as the type; and it is clearly adult. (As noted above, p. 92, the present author in 1951 ventured the opinion that SLADEN's *S. armatus* might be a juvenile specimen).

The superomarginal plates number 11-12 in the two arms preserved, and join their opposites from plates no. 4. (The specimen is very mutilated). The superomarginals of the disk are subquadrate, whereas those of the arms are much lower and rectangular, the proximal ones up to twice as long as high (fig. 21*a*). The inferomarginals of the arms are about half as high as their superomarginal companions and thus about three times as long as high. The surface of the marginal plates is granulated, corresponding to what is shown in SLADEN's fig. 4 pl. 28. The superomarginals of either side of the arms are fairly regularly opposite each other, and also the inferomarginals correspond regularly with the accompanying superomarginals.

Each arm bears a continuous row of 8-9 dorsal spines, gradually diminishing in size towards the tip of the arms (as is shown by the sizes of their basal knobs on the plates). The proximal arm spine is borne on one of the superomarginals of the first joining pair, as typical in *Styracaster*, and the following ones are then developed on successive pairs of joining plates, either alternatingly on either side of the arm, or on successive plates of the same side of the arm. Occasionally the two plates in an opposite pair each has a spine developed, but then one spine is always much smaller than its partner. All arm spines are lost in the specimen except a single proximal one, which is slender straight pointed and may have measured about 9 mm (being 8 mm long with the tip broken). The spine is borne on an about 1 mm high knob or protuberance on the superomarginal plate. The arms are very distinctly laterally compressed due to the ambulacral furrow being completely closed. (The arms in the type-specimen are described as subcylindroid). The compressed arms are about 4 mm high at their base.

There are in each interradius three cribriform organs of a rather sublamelliform structure.

The terminal ossicle is distal to the arm end, fairly inconspicuous, rather globular, and with 3 spines, a distal terminal one and a pair of smaller subterminal ones (fig. 21*b*).

The dorsal area shows the leathery integument mentioned by SLADEN. This covers an armature of small rounded plates, about 1/4 mm in diameter, of which those in the radial areas, extending from the arm bases halfway to the center of the disk, are naked, whereas the others bear 1-2, occasionally 3 spines each (about 0.2 mm long and about one-third as wide), (fig. 21*g, h*). There is a faint central elevation with smaller plates and spinelets. The madreporic body is conspicuous, round, close to the marginals, and with the striae radiating from an adcentral point. Papulae were not observed.

The adambulacral ossicles number 24-25. The proximal ones are subrhomboid, otherwise they are elongate, vertebra-shaped as SLADEN very appropriately describes them, with an excave furrow margin, and in the arms with a convex interradial margin. The proximal 1-2 adambulacralia bear 4 pointed flattened furrow spines of which the adoral one is much larger than the others, and further 1-3 subambulacral spines side by side near the adoral margin (fig. 21*c*). The following adambulacralia bear 3 (-4) furrow spines and 1, exceptionally 2, subambulacral spines adorally, and from about the seventh adambulacral ossicle the armature consists of two diverging conical pointed furrow spines on the adoral part of the margin, and an almost equally large subambulacral spine near the interradial adoral

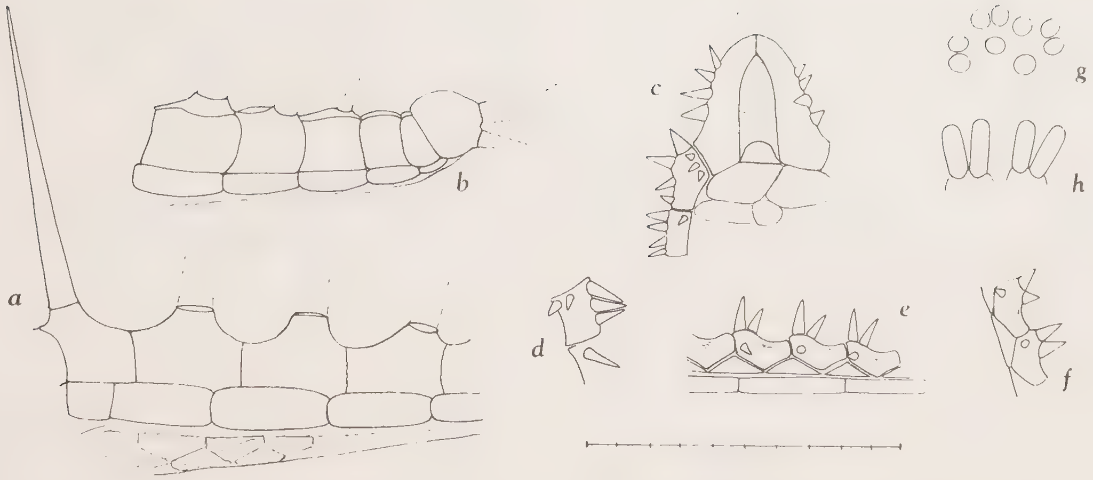

Fig. 21. *Styracaster armatus*. St. 280, R/r 39/13 mm; a, proximal part of arm, showing the superomarginals nos. 4-7; b, distal part of another arm, partly with the granulated surce indicated; c, jaw, with the mouth-spines reconstructed; d, an adambulacral ossicle no. 2; e, adambulacralia nos. 9-11, shown with their surface in the plane of the paper; f, adambulacralia from the median part of another arm; g-h, paxillar spinelets in dorsal view and in lateral view, in four times the usual scale. Scale: 10 mm (in g-h: 2.5 mm).

corner (fig. 21*e*). The triangular ends of the adambulacral ossicles, observable in the arms dorsally to the adambulacralia, are very wide in this species, actually touching each other in a continuous series.

The oral ossicles of each pair forming a jaw (fig. 21*c*) only join proximally, and are separated for the greater part of their length by a broad suture, as broad as the semicircular exposed surface of the primary oral ossicle. This appearance of the oralia is apparently an important taxonomical characteristic of the species. Each oral ossicle has carried a larger spine at its tip (lost in the few oralia preserved, the greater part of the oral area of the specimen having been torn away), and laterally at a small distance from the tip there is a series of 4-5 smaller conical and pointed marginal spines. Medially on their surface the oralia may bear a single suboral spine or up to 3 spinelets.

The ventrolateral plates are arranged in about 10 tangential rows, and in the outer half of the disk area also in radiating series, two of these usually corresponding with a marginal plate. The more distal ventrolateral plates are transversely elongate to subhexagonal and the more proximal ones, as usual, larger and irregularly shaped. SLADEN described the ventrolateral plates as imbricating, but in the present, apparently more expanded specimen this applies only to the plates near the margin. The ventrolateral plates are naked. They are of a very porous structure (as seen when the thin covering integument is rubbed off).

Distribution:

Styracaster armatus is known from four dredgings (fig. 37): one in the western tropical mid-Pacific, near the Caroline Islands, and three in the Indian Ocean in the Bay of Bengal and south of Ceylon. It is taken in depths between 3365 and 4350 m, and always on a bottom of globigerina ooze. The temperatures recorded are 1.3° and 1.9° C.

Styracaster spinosus E. Perrier, 1885

Machairaster pictus n. sp., E. PERRIER 1884 p. 272 (nom. nud.).

Styracaster spinosus n. sp., E. PERRIER 1885*a* p. 886 (nom. nud.); 1885*b* pp. 55-59; 1894 pp. 223-227, pl. $17_{2\,\text{a-d}}$.

Styracaster spinosus, KOEHLER 1909*b*, pp. 39-40.

Styracaster edwardsi n. sp., E. PERRIER 1885*a* p. 886 (nom. nud.); 1885*b* pp. 59-60; 1894 pp. 220-223, pl. $17_{3\,\text{a-e}}$.

E. PERRIER in 1884 mentioned a new form of sea-star, *Machairaster pictus*, related to *Porcellanaster*, but distinguished by having keeled arms with spines. In a subsequent paper (1885*b*) he described the form in detail, stating that the genus which it represents is that described as *Styracaster* by SLADEN in 1883, and that the form, which he now (by a lapse?) names by the specific name *spinosus*, stands near SLADEN's *Styracaster armatus*. In the final edition (1894) of this paper some figures are added. (SLADEN in 1889 p. 149 notes that *Machairaster* may perhaps prove to belong to *Styracaster*. Thus he had not seen PERRIER's paper of 1885 before in 1886 finishing his manuscript on the Challenger seastars).

The description of *Styracaster spinosus* was based on two specimens collected by the Talisman near the Azores (st. 131: 38°38′N, 27°26′W, 2995 m, soft white mud). The type-specimen has R/r 27/10 mm; 10 superomarginal plates, joining their opposites from plates no. 4, proximal one higher than long, following ones subquadrangular, and those of arms somewhat longer than high (in about the proportion 3/2); a continuous row of 5 arm spines; 3 cribriform organs; terminal ossicle with 3 spines. Dorsal side with a uniform covering of single spinelets, except for a triangular area at each arm base where no spines are developed; a distinct short apical appendage. Adambulacralia with a concave furrow margin and 3 triangular flat pointed furrow spines, two close together and diverging on the adoral broader part of the ossicle, and an isolated aboral one on the narrower part, further 1-2 conical subambulacral spinelets adorally. Oralia joining their opposites proximally and medially, at the primary oral ossicle, between the two places of contact a broad suture; each ossicle with 5 flattened triangular pointed marginal spines, proximal one the largest, and 3-4 suboral spinelets distally. Ventrolateral plates naked, in about 5 tangential and 8 radial rows. A series of isolated ventrolateral plates extending into arms.

KOEHLER in 1909 adds the records of four specimens of *Styracaster spinosus* from three dredgings of the Princesse Alice in the same area as the type-locality, in the eastern Atlantic near the Azores (st. 527: 38°09′N, 23°17′W, 4020 m; st. 745: 38°05′N, 23°50′W, 3465 m, muddy sand; and st. 753: 39°52′N, 18°01′W, 4360 m, globigerina ooze). These specimens have R/r 42/13, (30-35)/10, (30-35)/8, and 22/10 mm respectively, the first mentioned with 14 and the last mentioned with 11 superomarginals. The largest specimen with 3 pointed furrow spines on the proximal 3-4 adambulacralia, and generally only 2 on the following ones; the smallest specimen with 3 furrow spines for the greater length of the arms. The large specimen with 9, the small one with 5-6 arm spines. All specimens with a distinct apical cone.

PERRIER in 1894 notes that his *Styracaster spinosus* is the Atlantic representative of the Pacific *S. armatus* described by SLADEN, but that it is distinguished from this by the shape of its oralia, and by its shorter superomarginal plates.

Styracaster edwardsi: This was described by E. PERRIER (1885) from a single specimen collected by the Talisman in the eastern Atlantic near the Cape Verde Islands (st. 102: 15°18′N, 22°43′W, 3655 m, grey mud). In all probability, however, it is identical with the species *S. spinosus*. The type of *S. edwardsi* has R/r 36/9 mm; 12 superomarginals, joining their opposites from no. 4, first two higher than long, following ones subquadrangular; a continuous row of 7-8 arm spines; 3 cribriform organs. Terminal ossicle elliptical, fairly conspicuous, with 4 spines, a larger distal terminal one, a pair of smaller subterminal ones, and a small median one dorsally. Disk with numerous blunt spinelets, each on its own small plate, but a triangular area at arm bases with naked plates. Madreporic body roundish, with striae radiating from the center. A small apical cone. Adambulacralia with 3 furrow spines, two close together adorally and one isolated aborally; and 1 (on the proximal ossicle 2) subambulacral spine(s) adorally. Oralia in contact with their opposites proximally and medially, with 5 marginal spines, and 4 suboral ones distally. Ventrolateral plates naked, transversely elongate, in about 10 tangential and 14 radial rows. A series of oblong ventrolateral plates extending in arms to marginals no. 6.

PERRIER (1894) notes that his species *Styracaster edwardsi* is close to *S. armatus* and *S. spinosus*, but has longer arms. The length of the arms in relation to the diameter of the disk, however, is usually a rather poor taxonomic character, and neither the different number of terminal spines in *S. spinosus* and *S. edwardsi*, nor that of the superomarginals and the arm spines are of any taxonomical importance. The flattened furrow spines are pointed in *S. spinosus* but blunt in *S. edwardsi*, but as is known from other species, also this may vary individually. The shape of the oral ossicles is the same in *S. spinosus* as in the former form. Thus the conclusion must be that PERRIER's *S. edwardsi* cannot be kept specifically distinct from his *S. spinosus*. *S. armatus*, as noted above, is distinguished from *S. edwardsi*, and thus also from *S. spinosus*, by having the two oralia of a jaw widely separate also medially.

KOEHLER in 1909 p. 38 writes that he has reexamined the specimens of *S. edwardsi* and *S. spinosus* with the possibility in mind that they might be juveniles of his *S. elongatus*, which he, however, found was not the case. The present author in a paper of 1951, however, did not want to exclude the possibility that *S. spinosus* and *S. edwardsi* were juvenile *S. elongatus*, but the range of variation observed in the different species of *Styracaster* during the study of the Galathea material has confirmed Koehler's view.

Distribution:

Styracaster spinosus (inclusive of *S. edwardsi*) is known from five dredgings in the western Atlantic (fig. 37), near the Azores and the Cape Verde Islands, in depths from 2995 to 4360 m, and on a bottom of mud, muddy sand or globigerina ooze.

Styracaster clavipes Wood-Mason & Alcock, 1891

Wood-Mason & Alcock 1891 *b* p. 434; (Alcock 1893 p. 86).

This species was described from a single specimen taken by the Investigator in the Bay of Bengal (st. 117: 11°58′N, 88°52′E, 3197 m, globigerina ooze, 1.7° C.) in this way: "Agrees with *S. armatus* very closely, but differs in the following particulars: – There are five cribriform organs...; the inferomarginals are not much longer than broad; the terminal plate ... is markedly inflated; the median spine of the ... rays are comparatively short and blunt."

From this very brief description it is difficult to form a definite opinion of the specimen. The larger number of cribriform organs in *S. clavipes* is alone of no distinguishing value. Information of the size of the specimen would have been of interest. The different shape of the infero-marginals, in *S. clavipes* "not much longer than broad", in *S. armatus* about three times as long as high, and the difference in the terminal ossicles, in *S. clavipes* "markedly inflated", in *S. armatus* inconspicuous, seem to be more reliable taxonomic characters. These characters are such as also distinguish Perrier's *S. spinosus* (inclusive of his *S. edwardsi*) from *S. armatus*, and therefore *S. clavipes* may prove to be identical with this latter species.

Styracaster monacanthus Ludwig, 1907

Ludwig 1907 p. 315.
H. L. Clark 1920 pp. 79-80, pl. 2_{1-2}.

This species was diagnosed by Ludwig on the basis of a single specimen from an Albatross dredging in the eastern tropical Pacific (st. 4701: 19°12′S, 102°24′W, 4143 m, dark brown clay, 1.9° C.). The specimen is later mentioned by H. L. Clark (1920) who also published two photographs of it, from the dorsal and the ventral side respectively.

The unique type has R/r $24/12^{1}/_{2}$ mm, the arms being very short and narrow in relation to the disk; 7 superomarginals, joining from no. 5; a single dorsal spine to each arm, on one of the 5th superomarginal plates; (interradial inferomarginals very low); 7 cribriform organs; terminal ossicle with 3 robust spines. Whole dorsal side of disk fairly closely armed with blunt spinelets, each on its own granula-like plate. No apical cone. Adambulacralia, about 16 in number, with 4 (sometimes 5) furrow spines, (scale-like according to the photo). Oralia with 9 scale-like marginal spines (oral and adambulacral armature thus modified as segmental papillae). (A suboral and subambulacral armature not present, at least not mentioned either by Ludwig or by Clark). Ventrolateral area with a pavement of uniformly sized (i. e. all fairly small) subhexagonal squamous naked plates.

H. L. Clark apparently considered *S. chuni* and *S. paucispinus* the nearest allies of *S. monacanthus*, which, however, may not be true. Among the other species of *Styracaster*, *S. monacanthus* probably agrees best with those of the *armatus* group, like these having only single spinelets on the dorsal plates (no paxillae), but, according to the photo published, differing by having a uniform armature of spinelets over the whole dorsal side, inclusive of the arm bases, where the species of the *armatus* group show a triangular area with naked plates only. *S. monacanthus*, everything considered, appears very well distinguished from all other known species of *Styracaster* by its general facies, with the very short and narrow arms. (A similar appearance is sometimes shown by individuals of other species in radii where lost arms are regenerating).

Porcellanaster Wyville Thomson, 1877, emend. Fisher, 1905

Type-species: *Porcellanaster cæruleus* Wyville Thomson, 1877.

Syn.: *Caulaster* E. Perrier, 1882 (type-species: *C. pedunculatus* E. Perrier, 1882).
Albatrossia Ludwig, 1905 (type-species: *A. semimarginalis* Ludwig, 1905).
Albatrossaster Ludwig, 1907 (new name to replace *Albatrossia*, erroneously considered invalid).

Diagnosis:

Porcellanasterids with opposite superomarginals separate in whole arm length, and possibly with dorsal spines. Terminal ossicle distal to arm end, not markedly broader than long. A mid-interradial suture. A single lamelliform cribriform organ. A single proximal mouth-spine, common to both oralia forming a jaw. Pedicellariae sometimes present dorsally on disk, and sometimes formed by the furrow spines.

Description:

The general shape is substellate with the arms rather broad, rounded, and only slightly tapering. The disk is rather gibbous, and of a tumid appearance in well-expanded specimens. Usually there is an apical appendage. Small spiniferous plates are distributed over the central dorsal area to an extent varying with age, but not farther than a line connecting the distal edges of the outermost cribriform organs. The integument of the arm bases and arms includes spaced perforated plates. In the ventrolateral area there is a pavement of plates which sometimes bear spinelets. The jaws are large and prominent and bear a few marginal spines besides the single larger one, standing at the junction of the two oralia. The adambulacralia are elongate and with a protruding adoral part on which the few (2-3) furrow spines are borne. The surface of the oralia and the adambulacralia is as a rule naked.

Remarks:

The generic name *Porcellanaster* was created by Wyville Thomson in 1877, in his popular account on the work of the Challenger Expedition in the Atlantic, for some sea-stars which were dredged off the coast of the United States of America, S. E. of New York, and which were the first representatives of the group of deep-sea sea-stars now known as the Porcellanasteridae. Wyville Thomson intended to report himself on the collection of sea-stars brought back by the Challenger Expedition,[1] but due to illness had to give it up, and Percy Sladen was entrusted with the work. In the Challenger report Sladen (1883, 1889) then described a total of six species of the genus *Porcellanaster,* inclusive of the *P. cæruleus* named by Wyville Thomson. Later authors have added to this number, so that now altogether 20 different species or nominal species (inclusive of subspecies) have been mentioned in or referred to the genus, though some of them originally classified under other generic names (*Caulaster, Albatrossia* (= *Albatrossaster*), and *Eremicaster*). The species or forms on which the genera *Caulaster* and *Albatrossia* were based by their authors (Perrier and Ludwig) thus by later revisors are considered juvenile stages of *Porcellanaster. Albatrossaster* was merely a new name created by Ludwig to replace *Albatrossia,* erroneusly believed invalid (see p. 134). *Eremicaster* was originally erected by Fisher as a subgenus of *Porcellanaster,* but was by Ludwig raised to the rank of a genus (but given a somewhat different circumscription), and also Fisher himself later considered *Eremicaster* (in his original sense) of generic rank.

As will be discussed in the following, the genus *Porcellanaster* in the sense of Sladen should be separated into the two groups: *Porcellanaster* emend. Fisher, and *Eremicaster* sensu Fisher.

The specific (and subspecific) names used in connection with the generic name of *Porcellanaster* are, listed in their chronological order:

cæruleus Wyville Thomson, 1877
pedunculatus (Caulaster) Perrier, 1882
caulifer Sladen, 1883
tuberosus Sladen, 1883
*_crassus_ Sladen, 1883
*_gracilis_ Sladen, 1883
sladeni (Caulaster) Perrier, 1885
inermis Perrier, 1885
granulosus Perrier, 1885
eremicus Sladen, 1889
*_pacificus_ Ludwig, 1905
*_waltharii_ Ludwig, 1905
semimarginalis (Albatrossia) Ludwig, 1905
nudus (_Albatrossaster_) Ludwig, 1907
*_vicinus_ Ludwig, 1907
*_inermis, vicinus_ var., Ludwig, 1907
dubius (_Caulaster_) Koehler, 1909
richardi (_Albatrossaster_) Koehler, 1909
fragilis Döderlein, 1921
irregularis Lieberkind, 1932

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[1] Wyville Thomsen in 1877 I p. 380 after having described the North West Atlantic type-specimen of *Porcellanaster cæruleus* notes that "This is a very widely distributed deep-water species. We met with it near Tristan d'Acunha in the Southern Sea, and in the North Pacific." The specimens referred to by Wyville Thomson were, however, described as different species by Sladen, viz: *Porcellanaster eremicus, P. crassus, P. gracilis,* and *P. tuberosus. P. crassus* and *P. gracilis* are now referred to *Eremicaster;* but, as appears from the following, the present author considers Sladen's *P. eremicus* and *P. tuberosus* inseparable from *P. cæruleus.*

Wyville Thomson further noted p. 380 that: "There is an allied species of the same genus somewhat more ornate, and of an orange instead of a blue colour in the China Sea". Perhaps this statement refers to the specimen described by Sladen as *Hyphalaster inermis.* The note (1877 II, p. 267) of "a new species of *Porcellanaster* remarkable for a series of long spines running along the centre of the back of each ray", refers to the species described by Sladen as *Styracaster horridus.*

All these forms have either one or three cribriform organs in each interradius. Those with only a single cribriform organ represent *Porcellanaster* s. str., and those with three cribriform organs (in the list marked with an asterisk) represent *Eremicaster* sensu Fisher. Also a few other, though not constant characters, may distinguish these two forms. Thus pedicellariae may occur in *Porcellanaster,* but have never been found in *Eremicaster*; and in *Eremicaster* the adambulacral spines may be modified as so-called segmental papillae, which are unknown in *Porcellanaster.*

The following nominal species of *Porcellanaster* s. str. are described from the Atlantic: *cæruleus, pedunculatus, sladeni, inermis, granulosus, eremicus, richardi,* and *irregularis*; from the Indian Ocean: *caulifer, dubius,* and *fragilis*; and from the Pacific: *tuberosus, semimarginalis,* and *nudus.*

Porcellanasterids referable to *Porcellanaster* s. str. were hitherto recorded from 79 dredgings: 66 in the Atlantic, six in the Indian Ocean, besides three in the region of the Malay Archipelago, and four in the Pacific. In the present paper is now added the description of 12 specimens collected by the Galathea Expedition in six dredgings, two of which in the Atlantic, two in the Indian Ocean, and two in the Pacific, and of two specimens available from a dredging by the Pickle of the South African Fishery Investigations.

The present author has had occasion to re-examine a good deal of the previously described specimens of *Porcellanaster,* viz. those collected by the Ingolf, the Thor, the Godthaab, and the Valdivia expeditions, and further he has himself reported on the specimens collected by the Swedish Deep-Sea Expedition, and has thus been able to study a total of 54 specimens of *Porcellanaster* from 17 widespread localities. Only about 25 of the remaining specimens known have been described in more or less detail, whereas the others are merely listed.

Porcellanaster s. str. is an intricate group, and much richer collections than are available at present, will be needed to obtain a clear concept of its taxonomy. The Galathea material includes specimens of all sizes, ranging from juveniles about as small as any hitherto on record, to specimens of the known maximum size (R/r about 36/11 mm) and apparently senescent. Several of the forms described in the literature are represented in the material at hand, and undoubtedly they are for the greater part only different stages of growth of one and the same form (*cæruleus*). Actually the present author has been quite unable to find any characters by which the specimens known of *Porcellanaster* s. str. might be separated with certainty into more species or subspecies, and therefore regards the genus as monotypic. It shows polymorphism, however, (cf. e. g. the description p. 140 of the two specimens dredged by the Pickle); and rather confusing it is that some specimens though they are juveniles in their skeleton, nevertheless seem to be sexually mature (*richardi* and *semimarginalis* e. g.). Perhaps these latter may represent a paedomorphic form of the typical *cæruleus.*

The type-species *P. cæruleus,* preliminarily described by Wyville Thomson in 1877, was given a more exhaustive description by Sladen in 1883 and 1889. (The original spelling of the specific name, *ceruleus,* was by Sladen emended to *cæruleus*). Several specimens were available, and Sladen also made a few notes on the infraspecific variation, but it is only in his remarks, in 1889, under his species *P. eremicus* that a few hints are given as to the changes with growth from the juvenile to the adult stage. Lieberkind in 1935, when dealing with the Ingolf specimens, is the only author who has given a more detailed account of the variation within the species, especially with growth during the young stages.

Lieberkind also discussed the other forms of *Porcellanaster* described in the course of time from the Atlantic, and re-examined several of them, and his conclusions were that most Atlantic specimens of *Porcellanaster* recorded, belonged to the species *P. cæruleus.* He excepts only E. Perrier's *P. granulosus*; which exception, however, as discussed in the following, he based on a misinterpretation of one of the anatomical features of the genus. Further Lieberkind did not take any final view on Koehler's *Albatrossaster richardi,* but if he is right in referring all the other forms to *P. cæruleus, A. richardi* can hardly form an exception. This latter view was also maintained by the present author in 1951 when some specimens of *Porcellanaster* from the Swedish Deep-Sea Expedition, agreeing with Koehler's description of *richardi,* were recorded under the name of *cæruleus*, Lieberkind, in 1935 in his discussion of the Atlantic records of *Porcellanaster,* did not mention his own *P. irregularis,* described in 1932 on the basis of some specimens from the Gulf of Guinea, but since it is not included in the list of synonyms of *P. cæruleus,* he may still regard it as a distinct form. The characters, however, which should separate *irregularis* from *cæruleus*, viz. irregularities in the arrangement of the marginal plates, are of no taxonomical value whatsoever.

The specimens of *Porcellanaster* recorded from the Indian Ocean and the Pacific were not discussed by Lieberkind, who only noted that Koehler's *Caulaster dubius*, and Ludwig's *Albatrossia semimarginalis* and *A. nudus*, are juveniles and not referable with certainty to species. (As will be discussed in the following, nothing can be found in the descriptions of these three forms to distinguish them with certainty from *P. cæruleus*). The other forms of *Porcellanaster* (from other oceans than the Atlantic) are Sladen's *P. caulifer* and *P. tuberosus*, and Döderlein's *P. fragilis* (and nothing is found in the description of these to distinguish them from *P. cæruleus*).

Porcellanaster cæruleus Wyville Thomson, 1877

Figs. 22-24

Porcellanaster ceruleus n. sp., Wyville Thomson 1877 pp. 378-380, figs. 97-98.

Porcellanaster cæruleus, Sladen 1883 pp. 218-222; 1889 pp. 134-138, pls. 20_{1-7}, $20A_{1-10}$.

Porcellanaster cæruleus, Verrill 1885 pp. 520, 543, figs. 40-41.

Porcellanaster, sp. prox. *cæruleus*, Wood-Mason & Alcock 1891*b* p. 434. (pro parte = *Caulaster dubius*, and (?) *P. caulifer* in Koehler 1909*a*).

Pars *Porcellanaster cæruleus*, Alcock 1893 p. 86 (see Wood-Mason & Alcock 1891*a*, *b*).

Porcellanaster cæruleus, Verrill 1895 p. 133.

Porcellanaster cæruleus, H. L. Clark 1923 p. 239.

Porcellanaster coeruleus, Lieberkind 1935 pp. 5-19, text-figs. 1-5, pls. 2_{1-8}, 3_{12}, 5_{16-17}.

Porcellanaster coeruleus, Madsen 1951 pp. 74-76, fig. 1.

Caulaster pedunculatus n. sp., E. Perrier 1882 pp. 1379-1381; 1885*b* pp. 45-47; 1894 pp. 204-208, pl. $15_{1\,a\text{-}e}$.

Porcellanaster caulifer n. sp., Sladen 1883 pp. 222-223; 1889 pp. 138-140, pls. 21_{5-10}, 27_{9-12}.

Porcellanaster caulifer, Koehler 1909*a* pp. 33-34, pls. 11_5, 13_1.

Porcellanaster tuberosus n. sp., Sladen 1883 pp. 223-225; 1889 pp. 140-141, pls. 23_{1-4}, 27_{13-16}.

Caulaster sladeni n. sp., E. Perrier 1885*a* p. 886 (nom. nud.); 1885*b*, pp. 47-50; 1894 pp. 208-210, pl. $15_{2b,\,3a\text{-}c}$ (pl. $15_{3a\text{-}c}$ by a lapse under the name of *Porcellanaster inermis*, non pl. $15_{2,\,2a,\,2c}$ which represent *inermis*, according to Lieberkind 1935).

Porcellanaster inermis n. sp., E. Perrier 1885*a* p. 886 (nom. nud.); 1885*b* pp. 50-53; 1894 pp. 212-215, pl. $15_{2,\,2a,\,2c}$ (by a lapse under the name of *Caulaster sladeni*; non pl. $15_{3\,a\text{-}c}$ which represent *Caulaster sladeni*, according to Lieberkind 1935).

Porcellanaster granulosus n. sp., E. Perrier 1885*a* p. 886 (nom. nud.); 1885*b* pp. 53-55; 1894 pp. 216-218, pl. $17_{1\,a\text{-}c}$. (Also figured by Filhol 1885 p. 215 fig. 67).

Porcellanaster eremicus n. sp., Sladen 1889 pp. 145-149, textfig.

Albatrossia semimarginalis n. sp., Ludwig 1905 pp. 97-100, pl. 6_{30-31}.

Albatrossaster nudus, Ludwig 1907 pp. 318-319.

Albatrossia nuda, H. L. Clark 1920 p. 81, pl. 2_{5-6}.

Caulaster dubius n. sp., Koehler 1909*a* pp. 34-36, pls. 1_5, 5_8, 11_4.

Albatrossaster richardi n. sp., Koehler 1909*b* pp. 25-28, pl. 19_{7-9}.

Porcellanaster fragilis n. sp., Döderlein 1921 pp. 15-16, pl. $3_{1-1\,g}$.

Porcellanaster irregularis n. sp., Lieberkind 1932 272-276, texfigs. 1-4, pls. 1_{1-2}, 3_{1-3}, 7_{5-6}.

Non: *Porcellanaster*, resembling *cæruleus*, Wood-Mason & Alcock 1891*a* p. 13. (= *Sidonaster* sp.).

Nec: *Porcellanaster cæruleus*, Wood-Mason & Alcock 1891*b* p. 433 (= *Sidonaster* sp.).

Wyville Thomson's description of *Porcellanaster cæruleus* was based on some specimens dredged by the Challenger S. E. of New York (st. 45: 38°34′N, 72°10′W, 2270 m, blue mud, 2.9°C.), and the generic name he gave the form indicated a feature which has proved to be very characteristic of the whole group to which the form belongs (the Porcellanasteridae), viz. the large marginal plates which "are clear white with somewhat of a porcellanous lustre", and the specific name the colour of the disk "ranging from a pale to a tolerably strong cobalt-blue". (Verrill 1885 p. 520 states about *Porcellanaster cæruleus* that "Its cærulean color is due only to the bluish mud, with which its large stomach is usually filled, showing through the translucent integument. The real color is buff or pale salmon"). Wyville Thomson rightly pointed out the relationship of *Porcellanaster* with *Ctenodiscus*. He also described correctly what he called the ornament, and which later by Sladen was named the cribriform organ, but he made a lapse in considering the central apical appendage the excretory opening. (He may have had before him, however, a specimen with the appendage broken, and thus showing an artificial hole simulating an anus).

Later SLADEN (1883, 1889) gave a more detailed description of the species, further recording it from two other neighbouring Challenger dredgings (st. 46: 40°17′N, 66°48′W, 2469 m, blue mud, 2.9°C.; and st. 47: 41°14′N, 65°45′W, 2451 m, blue mud). The type-specimen of *Porcellanaster cæruleus,* according to SLADEN, has R/r 22/10.5 mm; 6-7 subquadrate superomarginals, generally armed with a short conical spinelet dorsally (innermost and penultimate plates naked); 6-7 (-8) inferomarginals, in arms somewhat lower than corresponding superomarginals, rectangular; 1 broad lamelliform cribriform organ; terminal ossicle fairly prominent, slightly tubercular, with proximal margin deeply indented and with 3 spines. Dorsal side of disk centrally and interradially with scattered minute plates, each with a spinelet. An apical appendage. Adambulacral ossicles with 2 pointed spines. A single proximal mouth-spine, common to both ossicles forming a jaw, and 2 small flattened lateral marginal spines to each side. Ventrolateral area with a compact pavement of naked plates, (in 4-5 tangential series and in radiating series three of which correspond in width with a marginal plate).

As type WYVILLE THOMSON has chosen a specimen (the largest one) with all the characteristics of a fully developed *Porcellanaster cæruleus,* but as appears from SLADEN's remarks, many of the other Challenger specimens do not show all these characteristics. The smallest specimen has R/r 8/4 mm, 4 unarmed superomarginals, and 4 (5) inferomarginals; spinelets on disk in definite interradial lines; a large apical appendage; and a complete pavement of plates ventrally. The subquadrate superomarginals are usually slightly longer than high, but in some specimens the proportions are reversed. Some larger specimens may have the superomarginal spines aborted, or absent altogether (or, in order words, rudimentary or not developed at all). Other specimens may bear spines on some of the ventrolateral plates. There may be 3 lateral oral spines (as is seen from fig. 2 pl. 20) and also 3 adambulacral ones.

VERRILL (1885 and 1895) recorded *Porcellanaster cæruleus* as taken in 42 hauls during the Albatross explorations in 1883 and 1884 off N. E. America, from 41°28′N to 37°50′N, at depths mainly from between about 1660 and 2750 m, but reaching 3520 m. He does not describe his material (only noted the colour, cf. p. 126), but he figures a specimen with R/r apparently about 14/6 mm, with 6 superomarginals armed with spines, and with spiniferous ventrolateral plates.

SLADEN (1889 p. 130) in the description of *Porcellanaster* notes that he has observed "that some of the small membrane-invested spinelets on the abactinal area are either cleft or double, and simulate the appearance of the sacculate pedicellariae in *Bathybiaster* ... They are generally situated near the marginal plates, and are usually most numerous in the neighbourhood of the madreporiform body." – This is evidently a reference to the pedicellariae found in some juvenile specimens of *Porcellanaster.*

A number of 32 specimens of *Porcellanaster,* the affinity of which with the species *cæruleus* is beyond doubt, was recorded and described by LIEBERKIND in 1935. Twenty-six of them were collected by the Ingolf in a dredging in the Davis Strait (st. 36: 61°50′N, 56°21′W, 2702 m, 1.5°C.), and in five dredgings in the Irminger Sea southwest of Iceland (st. 10: 64°24′N, 28°50′W, 1484 m, globigerina clay, 3.5°C.; st. 11: 64°34′N, 31°12′W, 2448 m, globigerina clay, 1.6°C.; st. 67: 61°30′N, 22°30′W, 1836 m, transition clay, 3.0°C.; st. 68: 62°06′N, 22°30′W, 1587 m, transition clay, 3.4°C.; and st. 83: 62°25′N, 28°30′W, globigerina clay, 1717 m, 3.5°C.). Four specimens were dredged by the Godthaab in the Davis Strait (st. 180: 62°07′N, 55°00′W, 2750 m, gray clay, 1.9°C.), and two were dredged by the Thor southwest of Ireland (st. 178: 48°04′N, 12°40′W, 1800 m). The largest North Atlantic specimen which LIEBERKIND had at disposal (Ingolf st. 36) had R/r about 13/5.5 mm; it has no superomarginal spines developed, but otherwise it agrees perfectly with the description of the type-specimen of *P. cæruleus.* Several of the other specimens from the same population were considerably smaller than any one mentioned from the Challenger material, and served LIEBERKIND in a survey of the changes in the dorsal skeleton with growth during the juvenile stages.

LIEBERKIND only recorded R/r for some of his specimens, e. g. those collected by the Godthaab which have R/r 6/3, 7/4, 8/5, and 9/5 mm. Other examples are (partly measured by the present author): Ingolf st. 10: 5.5/4 and 6/3 mm; Ingolf st. 36: 2.5/1.5-2, 3/2, 3/2, 3.5/2.5, 4/3, 6/2.5, 6-7/3, and 13/5.5 mm; Ingolf st. 67: 7/3 mm; Ingolf st. 68: 6/3 mm; Ingolf st. 83: about 1.5-2/1.5 mm and six specimens about 6-7/2-3 mm; and Thor st. 178: (5-)6/2.5 and 9/3 mm.

On basis of the description of the Challenger specimens, and of the Ingolf and the Thor specimens (which the present author has been able to reexamine), the following tabular survey is made

Tabular survey of the growth-changes in *Porcellanaster cæruleus.*

Specimen No.	Population	References to figures	R/r in mm	Number of plates			Supero-marginal spines	Ventro-lateral plates	Dorsal embryonic plates
				supero-marg.	infero-marg.	adambulacral.			
I	Ingolf st. 83	–	< 2/?	2	1	7	÷	÷	+
II	Ingolf st. 36	Lieberkind, fig. 1 B, pl. 2_2	2.5/1.5-2	2	1	4	÷	÷	+
III	Ingolf st. 36	Lieberkind, fig. 1 A, pl. 2_2	3/2	2	2	5	÷	+	+
IV	Ingolf st. 36	Lieberkind, fig. 1 C	3-4/2	3	2-3	6-7	÷	÷	+
V	Ingolf st. 36	Lieberkind, fig. 1 D, pl. 2_3	3.5/2.5	3	3	8	÷	÷	(+)
VI	Ingolf st. 36	Lieberkind, pl. 2_5	6/2.5	3	3	11	÷	÷	(+)
VII	Ingolf st. 36	Lieberkind, pl. 2_6	6-7/3	4	2-4	11	÷	(+)	÷
VIII	Thor st. 178	–	(5-)6/2.5	3	3-4	10-11	÷	÷	(÷)
IX	Challenger	Sladen, pl. 20_{6-7}	8/4	4	4-5	10-11	÷	+	÷
X	Thor st. 178	–	9/3	5-6	5	12	÷	(+)	÷
XI	Ingolf st. 36	Lieberkind, pl. 2_{7-8}	13/5.5	4	5	12	÷	+	÷
XII	Challenger	Sladen, pl. 20 A_{1-2}	ca. 17/8	5-6	5	15	+	+	÷
XIII	Challenger	Sladen, pl. 20_{1-2}	ca. 18/8	6	7	17	+	+	÷
XIV	Challenger	Wyv. Thomson, figs. 97-98 (Type-specimen)	22/10.5	6-7	6-8	(15-17)	+	+	÷

in order to show how some of the features of *Porcellanaster* change with growth. Half of the specimens listed in the table belong to the same population (Ingolf st. 36), and there should be no doubt as to the specific identity of the other specimens listed with those from this population. (The measurements given of the Challenger specimens are based in part on the published figures).

The information of the variation evident from this tabular survey may be supplemented with the following notes.

The superomarginal plates are rectangular in the very small specimens, and may also be so in specimens with R 13 mm, but in general they are subquadrate in specimens with R about 8 mm or more. They are unarmed in all the specimens described by Lieberkind, while in the larger Challenger specimens (R ≧ 17 mm) those of the proximal part of the arms each bears a small dorsal spine. (To judge from the figure of an Albatross specimen published by Verrill in 1885, also somewhat smaller North West Atlantic specimens (R about 14 mm?) may have superomarginal spines).

Cribriform organs are not yet developed in specimen no. II. Specimens nos. I and IV show a rudimentary cribriform organ in the interradius with the madreporite. Specimen no. III shows a rudimentary cribriform organ in all five interradii, and so does specimen no. V. All larger specimens have a well marked cribriform organ in each interradius.

The terminal ossicle is very dominating in the smallest specimens, but becomes relatively more inconspicuous with increasing size of the specimens. Usually there are 3 terminal spines, but some ossicles have the usual distal terminal spine replaced by two close-set ones, side by side, and thus are provided with 4 spines. This is e. g. the case in some terminal ossicles in specimens nos. I and VII. Occasionally a terminal ossicle carries 5 spines, viz. besides the usual 3 spines, an additional pair proximally on the dorsal surface.

The embryonic plating of the dorsal side is well distinct in the smallest specimens, the central area of the disk here being completely paved with large rounded, perforated plates. In specimens nos. V and VI the central embryonic plates are more or less absorbed, whereas there are still remnants on embryonic plates discernible in the arms. In the specimens with R 6-7 mm or larger, no traces of the embryonic plates are to be found any longer, and instead there is developed a dorsal skeleton of scattered small rounded plates, each carrying a single spinelet. These small spine-bearing plates first appear interradially near the margin, and thereafter spread along the interradial lines to the center of the disk. In specimens nos. IX to XI there are thus five distinct interradial bands of spinelets. In the larger specimens the spinelet-bearing plates eventually become distributed over the whole main disk area to a curved line connecting the distal corners of the first superomarginal plates. The dorsal spinelets are clothed in a sheat of skin which may reach considerably beyond their tip.

A few pedicellariae occur dorsally, interradially and centrally, in specimens nos. VI and VII. (Also some of the specimens described by Lieberkind from the Godthaab st. 180 are provided with a few dorsal pedicellariae, but all the other specimens and also those listed here from the Challenger material are without pedicellariae).

Pedicellariae are in the whole group of Porcellanasteridae known only from the genus *Porcellanaster* s. str. Lieberkind in 1935, when recording pedicellariae from three of his juvenile specimens, wrote that they were found earlier in only two other forms: *Caulaster dubius* Koehler and *Albatrossaster* Ludwig. This, however, is not quite correct, since pedicellariae were recorded also by Perrier from his *Caulaster pedunculatus*, and in the genus *Albatrossaster* (= *Albatrossia*) were recorded only from Koehler's *A. richardi*, but not from any of the two Pacific species described by Ludwig (*nudus* and *semimarginalis*). And, as noted above, p. 127, already Sladen in 1889 indicated the occurrence of pedicellariae in some of the Challenger specimens of *Porcellanaster cæruleus*. It appears that all specimens hitherto recorded with dorsal pedicellariae are juvenile, and the possession of pedicellariae thus may be a juvenile feature, the pedicellariae perhaps being lost with age.

The adambulacralia bear 2 (rarely 3) spiniform or more or less flattened furrow spines on their protruding adoral part. In specimen no. II the adambulacral armature of two flattened and slightly hollowed close-set subequal spines form a pedicellaria. (The same is the case in a specimen from Ingolf st. 67 with R/r 7/3 mm, and in one from st. 68 with R/r 6/3 mm).

The oral ossicles, besides the conical pointed mouth-spine common to both ossicles forming a jaw, bear 2 (rarely 3) lateral spines, spiniform and more or less flattened. (The lateral oral spines in some cases may form pedicellariae as the adambulacral ones, and quite exceptionally they may tend to appear as segmental papillae, cf. pp. 140 and 142).

The ventrolateral area in the small specimens is usually provided only with an integument devoid of any skeleton so that the calcified stone-canal shines distinctly through. In the smallest specimens the inferomarginal skeleton lies close to the adambulacral and oral ossicles. In specimens with R about 8 mm and larger ones there is generally ventrolaterally a complete pavement of close-set polygonal (subhexagonal) plates. Also smaller specimens, however, may sometimes be provided with ventrolateral plates, thus e. g. specimen no. III in which two fairly large plates fill out the whole ventrolateral area in the interradius with the madreporite, (the other interradii being still without any skeleton). Specimens as large as R 9 mm may have only a rudimentary ventrolateral skeleton, in specimen no. X e. g. consisting of two minute plates in each interradius, one to each side of the interradial midline (cf. fig. 4 in Lieberkind 1935), and all provided with a single spinelet. (The ventrolateral plates are otherwise generally naked in the Ingolf material; only one other specimen, st. 67 R/r 7/3 mm, has also some ventrolateral spinelets). The occurrence of ventrolateral spines is not correlated with the size of the specimens. Ventrolateral spines are recorded from specimens in the Challenger material, but all the large specimens figured are devoid thereof.

In the following discussion of the specimens of *Porcellanaster* described in the literature, the adult ones, for the sake of convenience, are treated first.

Porcellanaster inermis was created by E. Perrier (1885, 1894) to receive four specimens dredged by the Talisman near the Azores and near the Cape Verde Islands respectively (st. 131: 38°38′N, 27°26′W, 2995 m, soft white mud; and st. 101: 16°38′N, 20°44′W, 3200 m, grey mud). R/r are 11/7 mm in one specimen. The number of superomarginals is 5 in three specimens and 4 in the fourth, and there are 6 and 5 inferomarginals respectively. The superomarginals are subquadrate, all unarmed in three specimens, but nos. 3 and 4 with a small dorsal spine in the fourth. Cribriform organs with 12-14 lamellae. Terminal ossicles with 3 spines. Main area of disk with minute plates with single spinelets. A distinct apical appendage. Adambulacralia with 2 diverging spines. Oralia with 3 lateral spines besides the mouth-spine. Ventrolateral area with a pavement of naked plates in up to 6 tangential rows.

Lieberkind (1935) re-examined one of the original specimens, and declared *inermis* to be identical with *cæruleus*. The specimens named *P. inermis* agree with the Ingolf specimen no. XI in the table p. 128.

Porcellanaster granulosus was erected by E. Perrier (1885, 1894) on the basis of five specimens from three Talisman dredgings near the Cape Verdes (st. 96: 19°18′N, 20°21′W, 2330-2320 m, greenish mud; st. 97: 19°12′N, 20°17′W, 2324 m, greenish grey mud; and st. 101: 16°38′N, 20°44′W, 3200 m, grey mud). The type-specimen has R/r 24/7 mm and 9 subquadrate superomarginals, another one has R about 20 mm and 8 superomarginals, and also the others are of similar size. All superomarginals, except the first and the last one, with a dorsal spine. Terminal ossicle with 3 spines. Main disk area with a uniform armature of minute plates with single spinelets. Distinct apical appendage. Adambulacralia with 2 flattened pointed spines. Oralia with 2-3 lateral spines besides the mouth-spine. Ventrolateral area with a pavement of naked plates in about 4 tangential rows.

LIEBERKIND (1935 p. 11), after having re-examined one of the original specimens of *Porcellanaster granulosus,* concluded that the form apparently represented a species different from *P. cæruleus:* "being distinguished by a greater number of marginals, a more developed dorsal skeleton, smaller and more numerous ventrolateral plates, and the adambulacral plates in the distal corner cut obliquely, and the lacking piece replaced by a separate triangular plate". With regard to this last feature LIEBERKIND writes: "This character was to be found on each plate, and presuming that a thorough investigation will prove its presence in the other specimens too, this character must be considered so peculiar that the species may be maintained." – These "peculiar triangular plates" noted by LIEBERKIND must, however, be the ends of the adambulacral ossicles (see p. 44), and so nothing is left to distinguish *granulosus* from *cæruleus,* a fact which escaped the present author's attention when in 1951 he reported on the porcellanasterids of the Swedish Deep-Sea Expedition, and in agreement with LIEBERKIND excepted *P. granulosus* from the synonyms of *P. cæruleus.* Actually the specimens recorded under the name of *granulosus* agree perfectly with the type-specimen of *cæruleus* listed as no. XV in the table p. 128.

Porcellanaster irregularis was described by LIEBERKIND (1932) on the basis of three large specimens dredged by the Valdivia off Liberia (st. 63: 2°56′N, 8°04′E, 2492 m, 2.6°C.). LIEBERKIND gave the dimensions of the type-specimen as R/r 33/11 mm (the present author by a re-examination of the specimen found the oral opening very widened, so that 30 mm perhaps would be a truer statement for the length of R). The number of superomarginals is 7 in the type, 8 in another specimen with R about 30 mm, and 6-7 in the third with R 27 mm. The proximal superomarginals are slightly higher than long, otherwise they are subquadrate, or – if subalternating with the inferomarginals – subpentagonal or subhexagonal. Each of the superomarginals nos. 2-5 bears a short pointed spinelet. Terminal ossicles with 3 spines, a distal terminal one, and either a pair of subterminal ones or a pair of proximal dorsal ones, (or, as a re-examination shows, both kinds present and thus 5 spines in all). Disk area with a uniform covering of spaced small perforated plates with single spinelets; in the arms slightly larger naked plates. An apical cone. Adambulacralia with 2 slender spines. Oralia with 2 slender lateral spines besides the proximal mouth-spine (this latter reduplicated on some ossicles). Ventrolateral area paved with naked plates. (About 6 ventrolateral plates adjoin the first inferomarginal one).

As the primarily distinguishing character for his new species, LIEBERKIND mentions the irregularity in the arrangement of the marginal plates. This character, however, cannot be considered of any taxonomic value, representing merely an individual variation. Another character, which according to LIEBERKIND should distinguish *P. irregularis* from *P. cæruleus,* viz. a denser dorsal armature, neither is of any specific value, but is simply what could be expected in specimens of *cæruleus* almost one-third larger than any other specimens known previously. A few similarly large specimens from the Galathea Expedition will be described in the following.

All three additional forms of *Porcellanaster* described from the Atlantic on adult specimens (*inermis, granulosus,* and *irregularis*) are thus without reservation to be referred to the type-species *cæruleus.* Before entering on the discussion of the remaining species described from the Atlantic, all on the basis of juvenile specimens (*pedunculatus, sladeni, eremicus,* and *richardi*), it seems most convenient, however, to discuss the forms described on adult specimens from the Indian Ocean and the Pacific (*caulifer, tuberosus,* and *fragilis*).

Porcellanaster caulifer was described by SLADEN (1883, 1889) on the basis of a single specimen collected by the Challenger in the Arafura Sea in the Malay Archipelago (st. 191: 5°41′S, 134°05′E, 1463 m, green mud, 4.2°C.). It has R/r 21/6.5 mm; 7 superomarginals; slightly longer than high, each armed with a dorsal spine. Terminal ossicles with 3-5 spines (a proximal pair sometimes present). Main area of disk with an armature of slightly clavate spinelets; scattered papulae; a large apical appendage. Adambulacralia (14-15 according to the figure) with 2 spines. Oralia with 3 lateral spines besides the mouth-spine. Ventrolateral area with naked plates.

KOEHLER (1909*a*) recorded under the name of *caulifer* about a dozen specimens of *Porcellanaster*, collected by the Investigator in four dredgings in the Indian Ocean, in the Arabian Sea (Gulf of Oman), south of Ceylon, and in the Bay of Bengal, respectively (st. 299: 23°43′N, 58°52′E, 2376 m, soft green mud, 2.2°C.; st. 300: 24°16′N, 60°26′E, 2130-2515 m, green mud, 1.8°C.; st. 316: 5°44′N, 80°06′E, 2744 m, green mud, 1.7°C.; and st. 111: 12°50′N, 90°52′E, 3044 m, globigerina ooze, 1.9°C.). (The specimen from st. 111 may have been one of those recorded as *Porcellanaster* prox. *cæruleus* by WOOD-MASON & ALCOCK 1891*b*, p. 434). KOEHLER's material comprised a few juvenile specimens, some with R 12-16 mm, and one with R about 22 mm. He does not give any description, apart from mentioning that some specimens, especially among the large ones, carry spines on the ventrolateral plates. He notes that this cannot be considered a specific character however, since SLADEN has recorded the occurrence of ventrolateral spines also in some specimens of *cæruleus* (KOEHLER by an error writes *caulifer*). The Galathea material includes some specimens of *Porcellanaster* which closely agree with SLADEN's and KOEHLER's descriptions of *P. caulifer*, and the conclusion drawn from the study of these is that the form cannot be upheld as specifically distinct from *cæruleus*. SLADEN pointed out as distinguishing characters e. g. the long apical appendage (but the length of this is of no taxonomic value at all) and the clavate spinelets on the disk (but slightly clavate spinelets on the disk is found also in some Atlantic specimens of *Porcellanaster*).

Porcellanaster tuberosus was described by SLADEN (1883, 1889) from a single specimen collected by the Challenger off southern Japan (st. 237: 34°37′N, 140°32′E, 3429 m, blue mud, 1.8°C.). SLADEN gives R/r as 18.5/6 mm (but judging from the drawings in the Challenger report, 15 mm would perhaps be a truer figure of R, the specimen being very much extended by a full stomach and having the arms curved over the disk). There are 4 rectangular superomarginal plates, nos. 2 and 3 armed with a short conical dorsal spine; 5 inferomarginals; a conspicuous terminal ossicle with 3 spines. Whole dorsal area of disk with spinelets; a distinct apical appendage. Adambulacralia (12-14 according to the figures) with 2 spines. Oralia with 2 lateral spines besides the proximal mouth-spine. A ventrolateral pavement of naked plates.

The specimen falls in the number of superomarginals in relation to size within the variation to be expected in *P. cæruleus;* and the only difference from the original material of this form to be pointed out, is the rectangular shape of the superomarginals. The present author has not seen any equal-sized North Atlantic specimens of *P. cæruleus* with just as distinctly rectangular superomarginals as in the type-specimen of *P. tuberosus;* but usually their shape is somewhat variable within the populations, and e. g. the type-specimen of *P. caulifer* has also rather rectangular superomarginals. This difference alone, therefore, cannot be considered of any decisive taxonomic importance. In its other characters the type-specimen of *P. tuberosus* is intermediate between the specimens of *P. cæruleus* listed in the table p. 128 as nos. XI and XII respectively.

Porcellanaster fragilis was erected by DÖDERLEIN in 1921 for three specimens collected by the Siboga in two dredgings in the region of the Malay Archipelago (st. 175: 2°38′S, 130°33′E, 1914 m, grey and green mud; and st. 211: 5°41′S, 120°46′E, 1158 m, grey mud). One specimen has R/r 12/4.5 mm and 6 superomarginals, another R/r 18/6 mm and 8 superomarginals. Superomarginals rather subquadrate, and each with a spine; inferomarginals in arms half as high as superomarginals. Dorsally small plates, in disk with single spinelets, in arms naked; distinct apical appendage. Adambulacralia (14 in number by R 18 mm) with 2 spines, distally in the arms only 1. Oralia with 2 lateral spines besides the proximal mouth-spine. Ventrolateral area with a few naked plates.

DÖDERLEIN notes that his new species is near *cæruleus*, but is distinguished – among other things, he says – by the longer arms and more complete spine-armature dorsally. Neither of these characters, which are the only ones which DÖDERLEIN mentions, are of any taxonomic value, however. In the description the only other feature of some interest is that of the adambulacral armature distally in the arms consisting of only a single spine (whereas in all other specimens of *Porcellanaster* known, there seem to be 2 spines, also on the rudimentary adambulacral ossicles below the terminal ossicles), but even if correctly described also this character cannot be sufficient for distinguishing *fragilis* as a separate species. *P. fragilis* may justly be included among the synonyms of *cæruleus*. (What DÖDERLEIN, 1921 p. 15, mentions as "erste Reihe von Ventrolateralplatten", are in fact the ends of the adambulacral ossicles;

and what he, when describing the ventrolateral plates, mentions as "eine unpaare von dreieckiger Gestalt" aborally to the oralia, is of course the ventral surface of the primary oral ossicle).

It will appear from these considerations that not a single one of the six forms of *Porcellanaster* described on adult specimens, is really specifically distinguishable from the type-species *cæruleus*. It remains now to consider the seven forms based on juvenile specimens; and first are discussed the four forms from the Atlantic: *pedunculatus, sladeni, eremicus,* and *richardi.*

Caulaster pedunculatus was erected by E. PERRIER in 1882 for two small sea-stars collected by the Travailleur in two dredgings in the Bay of Biscay north of Spain (1880 st. 10: "au large de Santander", 1960 m; and 1881 st. 4, 43°N, 9°37′W, 2020 m, mud). (The depth of the latter dredging was in 1882 given as 2650 m, in 1885 as 2400-2600 m, and eventually in 1894 as 2020 m, apparently due to a confusion of the trawling no. 4 in 1881 with no. 4 in 1880). The two specimens have R/r 3/2 and 5/3 mm respectively; 3 superomarginals, 3 distinctly lower inferomarginals; narrow cribriform organs. Terminal ossicles conspicuous, with a proximal notch and 3 spines. Dorsal side with embryonic plates, large and distinct in the small specimens, indistinct in the large one, in which there is also a double row of spinelets in each interradial line. A conspicuous apical appendage. Dorsal pedicellariae. Adambulacralia (10 in the large one) with two lanceolate spines. Oralia usually with 2 flattened and pointed lateral spines besides the mouth-spine (judging from the figures and the somewhat obscure text, the armature may vary on the different oralia as is also known in other specimens of *Porcellanaster,* the mouth-spine apparently may be reduplicated, and there may be a third spiniform spine on the proximal lateral corner of the ossicle, or only a single oral spine laterally). Ventrolateral area with a tangential row of plates.

SLADEN in 1883, p. 217, and somewhat more detailed in 1889, pp. 130-131, expressed the opinion that *Caulaster pedunculatus* is a juvenile *Porcellanaster*. PERRIER in 1894, however, maintained his genus *Caulaster,* and described also an additional species, *C. sladeni.* LUDWIG (1907 p. 318) considered *C. pedunculatus* a juvenile *P. cæruleus,* and LIEBERKIND in 1935, after having re-examined one of the original specimens, confirms this view. The smallest specimen will be found rather to agree with the juvenile *cæruleus* no. III in the table p. 128, and the large specimen is intermediate between the specimens nos. VI and VII.

Caulaster sladeni was erected by E. PERRIER (1885*b*, 1894) on the basis of two specimens dredged by the Talisman off Morocco (st. 30: 32°38′N, 12°09′W, 1900-1435 m, sand and mud). R/r 10/5 mm; 4 (-5?) rectangular superomarginals, 4 somewhat lower inferomarginals; cribriform organs with 8-10 lamellae. Conspicuous terminal ossicle with 3 spines. Dorsal side with irregular (double) interradial rows of minute plates with spinelets; no embryonic plates; an apical appendage. Adambulacralia with 2 spines. Oralia with 3 lateral spines besides the proximal mouth-spine (the latter sometimes reduplicated?). Ventrolateral area with a few plates in two tangential rows.

LUDWIG in 1907, p. 318, expressed the opinion that this form was the juvenile *Porcellanaster inermis*. LIEBERKIND in 1935, after having re-examined a couple of the original specimens of *C. sladeni* and *C. inermis*, arrived at the conclusion that the former was a juvenile and the latter a small specimen of *P. cæruleus*. The specimens will be found to agree with the specimens of *P. cæruleus* listed as nos. IX and X in the table p. 128.

PERRIER mentions (1894 p. 210) a pair of small membraneous papillae at the base of the arms of his *Caulaster sladeni* as "peuvent être soit de papilles respiratoires, soit les orifices des organes génitaux". These are the gonad papillae, which are also observable in some of the juvenile specimens of *Porcellanaster* in the Galathea material (cf. fig. 24*c. o*).

Porcellanaster eremicus was erected by SLADEN in 1889 for a single juvenile specimen dredged by the Challenger in the southern Atlantic west of Cape (st. 137: 35°59′S, 1°34′E, 4664 m, red clay, 1.4°C.). R/r 6.5/3.2 mm; 4 rectangular superomarginals, 3 inferomarginals; terminal ossicle fairly conspicuous, with 3 spines. Dorsal side with a plating of large subcircular or oval perforated embryonic plates. Adambulacralia with 2 flattened lanceolate spines. Oralia markedly coulter-shaped, with 2 lateral spines besides the mouth-spine. No ventrolateral plates.

SLADEN notes that the specimen is "at a very early stage of growth" and "appears to be nearly related to *Porcellanaster cæruleus*". He did not really find any characters reliable for distinguishing it from *cæruleus,* the only difference noted being that the arms "are longer more attenuate and thinner throughout”, and when he, nevertheless, recorded the specimen as representing a new species, it was on account of the distance between the Challenger finds of *cæruleus* and of the present specimen, and further since “this course will also facilitate reference”.

Ludwig in 1907, p. 318, states that he considers *eremicus* a juvenile *cæruleus*, and H. L. Clark in 1923 and Lieberkind in 1935 are of the same opinion.

It is evident that *Porcellanaster eremicus* is very closely related to the North-Atlantic *cæruleus*, but it differs slightly from the population from e. g. the Ingolf st. 36 (cf. the table p. 128) in having retained a complete dorsal embryonic plating up to a somewhat larger size. (See further p. 134).

H. L. Clark in 1923 recorded four juvenile *Porcellanaster cæruleus* (R 7-9 mm) from two dredgings of the “Pieter Faure” in the Cape region (Cape Point N. E. by E. 1/4 E., 40 miles, 1460-1650 m, green mud; and Cape Point N. 83°E., 43 miles, 1650-1830 m, grey mud).

Clark notes that these specimens “are too young to make their specific identity certain but comparison with somewhat larger specimens of *cæruleus*, taken by the Challenger and the Blake, indicates that they are immature examples of that species”. (He also says that “On account of the locality it would be natural to refer these specimens to *P. eremicus* Sladen, but I (Clark) am myself satisfied that the specimen on which that species is based, is a young *cæruleus*”). A couple of specimens subequal-sized with Sladen’s *eremicus* and H. L. Clark’s *cæruleus* and also from the Cape region, will be described in detail in the following.

Albatrossaster richardi was erected by Koehler in 1909*b* for a single specimen dredged in the tropical mid-Atlantic by the Princesse Alice (st. 1173: 12°08′N, 33°33′W, 6035 m), and erroneusly listed under the name of *Hyphalaster parfaiti* by Albert in 1902 p. 962, and by Richard in 1902 p. 86. (The genus *Albatrossaster* was erected by Ludwig in 1905, and is discussed below). The specimen has R/r 10/4 mm; 5 rectangular superomarginals, 2-3-4 rudimentary inferomarginals; prominent terminal ossicle with 3 spines. A close pavement of rounded plates dorsally on disk, smaller plates in arms. According to Koehler p. 26 the dorsal plates “montrent à leur surface un dessin très régulier et élégant formé par des granules trés fins et aplatis disposés en mosaique”. This description, however, to judge from the condition in other juvenile specimens of *Porcellanaster*, must be incorrect, being an erroneous interpretation of the appearance under the lens of the perforated embryonic plates. *A. richardi* further has dorsally some pedicellariae in interradial groups of 4-5, and a long apical appendage. Adambulacralia (13-14 in number) with 2 spines, forming a pedicellaria which can be laid down in a pit on the ossicle. Oralia with 2-3 (the figure shows 1-2) lateral pedicellariae similar to the adambulacral ones. Ventrolateral area with some small spaced plates. (Koehler notes that the opposite superomarginals of the fourth pair touch each other distally, and that those of the fifth pair meet each other in their whole length, which, however, must be a matter of contraction).

Lieberkind in 1935, p. 16, discussed *Albatrossaster richardi* and concluded that it undoubtedly represented an immature stage of a *Porcellanaster*, as he knew such from the Ingolf collections, but that a richer material of the form from neighbouring localities would be required to decide whether it belonged to *P. cæruleus* or to another species.

In 1951 the present author reported, under the name of *P. cæruleus*, on five small specimens dredged in the mid-Atlantic west of the Cape Verde Islands by the Swedish Deep-Sea Expedition (st. 329: 9°44′N, 26°25′W, 5610-5600 m, calcareous red clay, 2.4°C.). They agreed in all essentials with Koehler’s *A. richardi*, and it was noted that the developmental stage they represent, corresponds with that of only about one-third as large North Atlantic specimens of *cæruleus*. Further it was suggested that the difference in size in relation to the developmental stage might be caused by a different food supply. This, of course, is a conjecture, and may be entirely unfounded. The size at which the embryonic plating of the dorsal side disappears – besides being subject to some individual variation – may perhaps be variable in different populations, without being influenced in any way by the environmental conditions. It may now be questioned, whether it was correct to go still further than Lieberkind, and consider *A. richardi* not merely a juvenile *Porcellanaster* but a juvenile *P. cæruleus*. A more detailed discussion of the specimens than given in 1951 may therefore be appropriate.

The five specimens of *Porcellanaster* from the Swedish Deep-Sea Expedition have R/r 8/3, 8/3, 9/4, 10/5, and 10.5/5 mm. There are 4 (in that with R/r 10/5 mm only 3) unarmed rectangular superomarginal plates, and 1-5 inferomarginal plates, their number being variable in the different arms as was also the case in the type-specimen of *A. richardi*. The dorsal side of the arms as well as of the disk is paved with small rounded perforated plates (embryonic plates). In the large specimens there are, however, also some spinelets interradially, near the margin. All the specimens are further provided with pedicellariae interradially and mainly near the margin, in a number of up to 10-12 in each interradius. There is a distinct, small apical appendage. The immature stage of the specimens is emphasized by the very small size of the madreporite in relation to the superomarginals. The cribriform organs are in some interradii still rudimentary, consisting of merely two "lamellae", whereas there are e. g. up to 6 lamellae in the cribriform organ in the interradius with the madreporite. The adambulacral ossicles number 11-14, and their armature is modified (like in the original specimen of *A. richardi*) as pedicellariae along the whole length of the arms, except on the most distal rudimentary ossicles. The oralia bear, besides the mouth-spine, 3 flattened lateral spines (instead of the pedicellaria in the type of *richardi*). The ventrolateral area is devoid of any skeleton. (The adambulacral pedicellariae are very peculiar and characteristic, but it is evident from the variation in the Ingolf populations of *Porcellanaster* that they are of no use taxonomically, at least not on the species level).

The dorsal aspect of the present specimens with R 8-10.5 mm, is the same as found in specimens of the Ingolf population with R 3-4 mm, but this apparently considerable gap is bridged by SLADEN's *P. eremicus*, which specimen with R 6.5 mm has a similar complete embryonic plating. Certainly KOEHLER's *richardi*, and the specimens discussed from the Swedish Deep-Sea Expedition, and probably also H. L. CLARK's *cæruleus* from near Cape, belong to the same form as Sladen's *eremicus*. Whether they are simply specifically identical with *cæruleus* is, however, difficult to decide definitely, but it is the most probable. Some specimens collected by the Galathea Expedition, and described below, agree perfectly with this group of *eremicus/richardi*.

Three forms of *Porcellanaster* based on juvenile specimens (*semimarginalis*, *nudus*, and *dubius*) are described from the Pacific and the Indian Ocean, and will be discussed in the following.

Albatrossia semimarginalis was established by LUDWIG in 1905 for the reception of two small specimens from two dredgings of the Albatross in the eastern tropical Pacific (st. 3362: 5°56'N, 85°11'W, 2149 m, green mud, sand and stone, 2.7°C; and st. 3371: 5°26'N, 86°05'W, 1408 m, globigerina ooze, 3.9°C.). They have R/r 11/5.5 and 9/4 mm respectively; 3 and 2 unarmed superomarginal plates, inferomarginals absent or rudimentary. In each interradius a cribriform organ with up to 20 lamellae. Terminal ossicle prominent, with 3 spines. Dorsal side with interradial bands of spinelets, each on a small perforated plate. An apical appendage, (Apparently no papulae). Adambulacralia (9 and 8 in number) with 2-3 spines. Oralia with 2 lateral spines besides the proximal mouth-spine. Ventrolateral area with spaced naked plates. (LUDWIG's statement: "dass die unteren Randplatten fast oder ganz in Wegfall gekommen sind" is incorrect in so far as the condition of course is the reverse, viz. that they are not yet distinctly developed).

LIEBERKIND in 1935 notes that this form is a juvenile *Porcellanaster*, but that the species it represents is undeterminable on basis of the available material alone. If compared with the specimens of *P. cæruleus* in the Ingolf populations, it is seen that *A. semimarginalis* has a slightly smaller number of superomarginal plates in relation to size than is the case in the Ingolf specimens, which, however, is a vague difference; and at least it appears impossible to distinguish *A. semimarginalis* from the specimens recorded as *eremicus/richardi*. A relatively small number of superomarginals is also found in the full-grown type-specimen of *P. tuberosus* (4 by R 18 mm) and e. g. also in the full-grown specimens of *Porcellanaster* from the Galathea st. 281 (5-6 by R 21-25 mm), which minimizes the significance of the character.

(Incidentally, LUDWIG in one of the specimens found eggs, 0.4 mm in diameter, and thus probably yet unripe, cf. p. 49).

Albatrossaster nudus was described by LUDWIG in 1907 from a single specimen collected by the Albatross in the eastern tropical Pacific (st. 4647: 4°33'S, 87°43'W, 3667 m, globigerina ooze, 1.9°C.), and in 1920 H. L. CLARK mentioned the same specimen and published some photos of it. (*Albatrossaster* was a new name created by LUDWIG in 1907 to replace his *Albatrossia* of 1905, in order to avoid confusion with *Albatrossa* (a bird), but as H. L. CLARK in 1920 notes, such a confusion does not seem probable – and in any case the name *Albatrossia* was not invalidated by the name *Albatrossa*). The type and only specimen known of *Albatrossia nuda* has R/r 7/4.5 mm; 2 unarmed rectangular superomarginals, 2 inferomarginals. Conspicuous terminal ossicle with 3 spines. Dorsal side with spinelets only interradially near the cribriform organs. Adambulacralia (8 in number to judge from the published photo) with 2 flat lanceolate spines, proximal ones apparently forming pedicellariae. Oralia with 2 similar lateral spines, besides the conical mouth-spine. Ventrolateral area paved with naked plates.

LUDWIG considers this specimen specifically distinguished from his *semimarginalis* by the almost complete absence of dorsal spinelets. But this character is merely depending on age, as demonstrated above in the survey of the changes with growth in populations of *Porcellanaster* from the North Atlantic. The specimen surely belongs to the same form as *Albatrossaster semimarginalis*, and the considerations made with regard to those specimens thus apply also to this one.

Caulaster dubius was erected by KOEHLER in 1909*a* for a small specimen dredged by the Investigator in the Bay of Bengal (st. 117: 11°58′N, 88°52′E, 3197 m, globigerina ooze, 1.8° C.) and belonging to the material recorded by WOOD-MASON & ALCOCK 1891*b* p. 434, as "*Porcellanaster* sp. proximate to *P. cæruleus*". It has R/r 5/2.5 mm; 3-4 rectangular superomarginals, and 3 narrower inferomarginals. Terminal ossicle conspicuous, with 3 spines. Dorsal side with spinelets in interradial bands, also 3-6 pedicellariae in each interradius. An apical appendage. Adambulacralia in a number of 8, with (2-)3 flattened spines. Oralia with 2 flat lateral spines (mouth-spine apparently lost in the specimen). Ventrolateral area without any skeleton.

LIEBERKIND in 1935, p. 11, briefly discussed this form, and supported KOEHLER in his view that it could not be the young of *P. caulifer*, "and in all probability neither a younger stage of other well-known forms of the genus *Porcellanaster* occurring in the Indian Ocean". The reasons for this conclusion are curious, however, since the specimen in fact agrees well with equal-sized specimens in North Atlantic populations of *P. cæruleus*, e. g. nos. VII and IX in the table p. 128, and may well be considered belonging to this species. (Incidentally, KOEHLER's reasons for reviving the generic name *Caulaster* are not in accordance with a strict nomenclatorical procedure and are rather vague, the main reason being that he considers the use of this name for the specimen most convenient, as he is not sure that it is a juvenile *Porcellanaster*, though – as he notes – it may well be so).

In the above, references have been made to all records of *Porcellanaster*, or forms belonging to this group, except to those given by WOOD-MASON & ALCOCK (1891*a* and *b*), and by ALCOCK (1893), of specimens collected by the Investigator. WOOD-MASON & ALCOCK thus in 1891*a*, p. 13, recorded from off Goa (st. 105: 1353 m) a small *Porcellanaster* "resembling in all important particulars *P. cæruleus*", and in 1891*b*, p. 433, they recorded a specimen of "*Porcellanaster cæruleus*" from the Andaman Sea (st. 113: 1249 m), and, p. 434, numerous small specimens of a "*Porcellanaster* sp. proximate to *P. cæruleus*" from the Bay of Bengal (st. 111 and st. 117: 3044 and 3197 m). ALCOCK in 1893, p. 86, finally added a record of *P. cæruleus* from the Laccadive Sea (st. 107: 1350 m). KOEHLER in 1909*b*, pp. 33-34, – with regard to these records – notes that, when examining the Investigator material sent to him, he did not find a single specimen belonging to *P. cæruleus*. Three specimens were labelled with that name, and KOEHLER confirms that one of them is a *Porcellanaster*, though too young and too damaged for a definite specific assignment. This specimen was from the Bay of Bengal (st. 111: 12°50′N, 90°52′E, 3044 m, globigerina ooze, 1.9° C.). Another specimen, from st. 117, is the one which KOEHLER described as *Caulaster dubius*. The third one, from st. 105, KOEHLER finds is a *Sidonaster*. It may here be added that in all probability also the specimen from st. 113 was a *Sidonaster*, considering that the bottom temperature at this station was 6° C., which temperature does not agree with the occurrence of a *Porcellanaster* (known temperature range: 1.1° to 4.2° C.), but fits well enough with the occurrence of a *Sidonaster* (known temperature range: 1.8° to 11.3° C.). The specimens from st. 111 are probably the same (in part) which KOEHLER records as *P. caulifer*. The only record of which no further information is available, is that of *P. cæruleus* from the Laccadive Sea (st. 107: 8°23′N, 75°47′E, 1350 m, green mud).

The material of *Porcellanaster:*

Specimens of *Porcellanaster* were collected by the Galathea in six dredgings: two in the Atlantic in the Gulf of Guinea, two in the Indian Ocean south of Ceylon, and two in the South Pacific, southwest of Australia and in the Kermadec Trench north of New Zealand respectively.

St. 52: 1°42'N, 7°51'W, 2550 m, ca. 3°C., muddy clay. 3 specimens.
St. 63: 2°00'N, 9°14'E, 1520 m, 3.8°C., blue clay. 1 specimen.
St. 281: 3°38'N, 78°15'E, 3310 m, 1.8°C., globigerina ooze. 3 specimens.
St. 282: 5°32'N, 78°41'E, 4040 m, 1.5°C., blackish mud. 1 specimen.
St. 574: 38°45'S, 159°39'E, 4670 m, 1.2°C. 1 specimen.
St. 664: 36°34'S, 178°57'W, 4540 m, 1.1 C., brown, sandy clay. 3 specimens.

A couple of specimens of *Porcellanaster* dredged near Cape by the Pickle of the South African Fishery Investigations are also available.

Pickle st. 92: 33°50'S, 17°59'E, 2176 m. 2 specimens.

The specimens from st. 52 in the Gulf of Guinea are equal-sized to, and in all characters closely agree with those from the same region described by Lieberkind as *P. irregularis*. They are by the present author considered full-grown (in part senescent) specimens of *P. cæruleus*. The small specimen from st. 63, also in the Gulf of Guinea, corresponds to those from off Morocco described by Perrier as *Caulaster sladeni*, which are considered juvenile *P. cæruleus*. The specimens from st. 281 south of Ceylon are fairly large ones which correspond to that from the Arafura Sea (Malay Archipelago) described by Sladen as *P. caulifer*, and to those from south of Ceylon later recorded under the same name by Koehler. They are by the present author also considered large specimens of *P. cæruleus*. The juvenile specimen from the neighbouring st. 282 agrees with the juvenile *caulifer* described by Koehler, as well as with Perrier's *sladeni*. The large specimens from sts. 52 and 281 have in preserved state still a faint purplish tint.

The two small specimens from Pickle st. 92 near Cape differ somewhat from each other in general appearance, one of them corresponding to Koehler's *Albatrossaster richardi* from the mid-Atlantic, the other to Perrier's *sladeni*. The single small specimen from st. 574 southwest of Australia and the three small ones from st. 664 in the Kermadec Trench, all correspond to that from the South Atlantic west of Cape, described by Sladen as *P. eremicus*. The present author is convinced that they too are juvenile *P. cæruleus*.

The specimens from Galathea st. 52, in the Gulf of Guinea. (Fig. 22):

The present three specimens have R/r 30/9, 32/11 and 36/11 mm respectively. The last mentioned is the largest specimen known of *Porcellanaster*, the hitherto largest one on record being Lieberkind's *P. irregularis* with R/r up to 33/11 mm (to which form these specimens, as noted, correspond), and the second largest Perrier's *P. granulosus* with R/r up to 24/7 mm. The number of superomarginals in the present three specimens is 8-9. The largest specimen shows a peculiar abnormality in that the ambulacral furrow and the ambulacral and adambulacral skeleton extend beyond the terminal ossicle (fig. 22*j*, *m*). The superomarginal plates all without exception are armed with a dorsal erect spine in one specimen, whereas in the other specimens the proximal one or two, and the ultimate and perhaps also the penultimate plates are unarmed. The spines are on the more proximal plates placed on their upper margin, but on the more distal plates the spine may be placed just a little lower. The first and second superomarginals may have their joining corners drawn out into a slight projection. (This is also sometimes the case in Lieberkind's material of *P. irregularis*).

The inferomarginal plates may lie exactly below their superomarginal companions for the greater length of the arms, or they may subalternate with these already from the plates nos. 2-3. Distally an irregular arrangement of the inferomarginal plates seems to be the usual. They are here generally shorter than the superomarginals; and as furthermore the distalmost one (or two) is developed earlier than its superomarginal partner, the number of inferomarginals may be up to 13-14. In addition a few supplementary plates may be pushed in here and there between the inferomarginal and superomarginal series. A similar irregularity in the arrangement of the inferomarginal plates was considered the main specific character of Lieberkind's *P. irregularis*, but such irregularities appear to be a frequent individual variation in various populations of porcellanasterids, and no taxonomic importance can be attached to the feature.

The cribriform organ comprises up to 26 folds, the supporting skeletal elements forming almost continuous lamellae, whereas the calcareous papillae of the covering rows are distinctly separate.

The armature of the terminal ossicles varies somewhat. In the smaller specimen there are 5 spines, a conical distal terminal one, a pair of

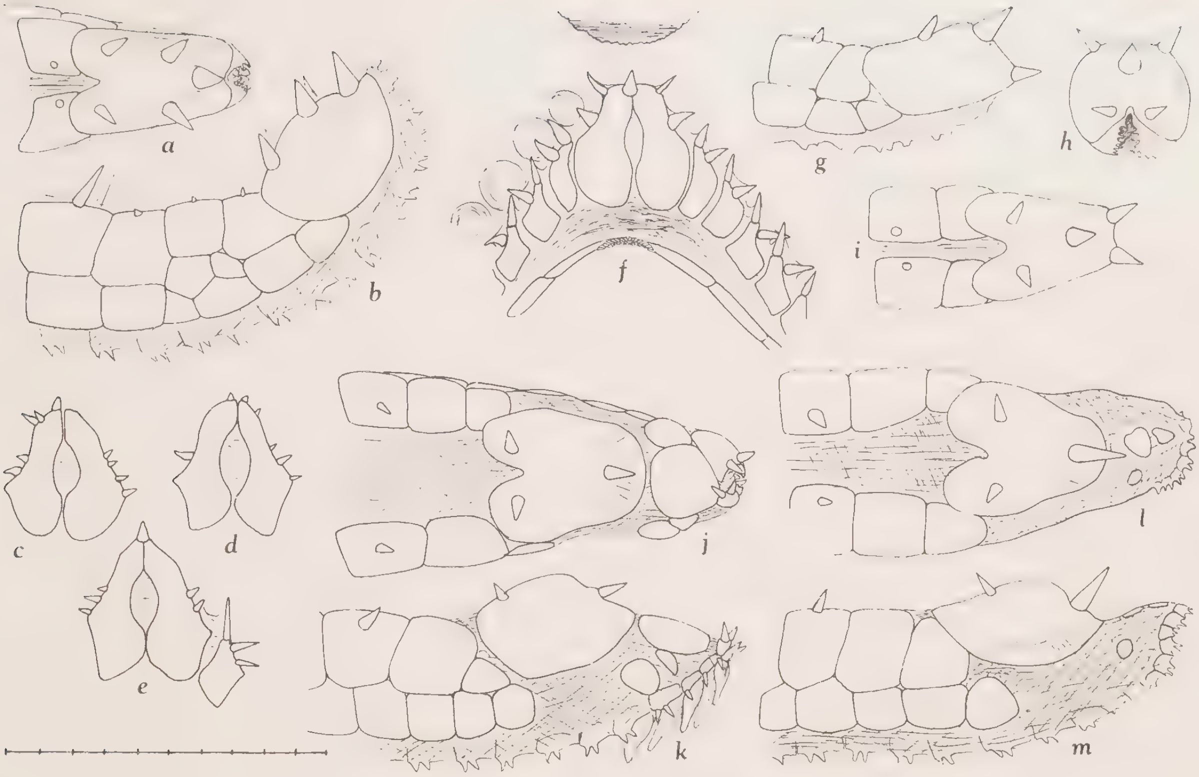

Fig. 22. *Porcellanaster cœruleus.* St. 52. a-e) R/r 32/11 mm; a-b, distal end of arm in dorsal view and in lateral view; c-e, different jaws. f-i) R/r 30/9 mm; g-i, a terminal ossicle in different views. j-m) R/r 36/11 mm; j-k and l-m, distal end of two arms in dorsal view and in lateral view respectively.
Scale: 10 mm.

slightly smaller subterminal ones, and a pair of small proximal dorsal ones (fig. 22*g-i*). In the medium-sized specimen there are also 5 spines, viz. the distal terminal one, and two pairs of slightly smaller proximal dorsal ones, whereas the usual subterminal pair is absent (fig. 22*a-b*). In the largest specimen there are 3 spines, the distal terminal one and a pair of proximal dorsal ones, the subterminal pair also here being absent (fig. 22*j-m*).

The dorsal side of the disk is provided with a fairly thick integument which – centrally and interradially, inside a line connecting the outer corners of the first superomarginal plates – is armed with uniformly scattered spinelets, each on its own small plate. All three specimens show a more or less distinct apical cone armed with minute spiniferous plates. The dorsal spinelets are rather spaced and not quite as numerous in the present specimens as they were in the slightly smaller type-specimen of LIEBERKIND's *irregularis*, but dorsal spinelets were sparser too in LIEBERKIND's two other almost as large specimens. The dorsal spinelets are mainly aciculate, but several, especially among those near the margin and near the arm bases, are terete, and some are slightly club-shaped, especially among those near the cribriform organs. In the smallest specimen the gonad papillae are observable near the corners of the cribriform organs. The madreporic body is circular, with a diameter about equal to the length of the first inferomarginal plate, and with the striae stretching across in radial direction or radiating from an adcentral point.

The adambulacral armature consists typically of 2 spiniform furrow spines, but in one specimen the first adambulacral ossicle, and also other scattered ones (no. 7 e. g.), may bear 3 furrow spines. The specimen with R/r 30/9 mm has 25-27 adambulacral ossicles.

The oral armature consists, besides of the conical proximal mouth-spine common to both the oralia forming a jaw, of 1-4 marginal spines laterally on each ossicle. In the smaller specimen there is thus 2 lateral conical spines subequal to the mouth-spine, one of them placed at the lateral proximal corner of the oral ossicle, the other near the corner adjacent to the adambulacralia (fig. 22*f*). In the largest specimen there is also generally 2 lateral spines on the oralia, though on one ossicle 3 such spines, viz. 2

small close-set ones distally, besides the one on the proximal lateral corner. In the medium-sized specimen the oral armature is fairly varying on different ossicles. Thus the usual unpaired mouth-spine may be replaced by 2 smaller spines, one to each oral ossicle in the jaw; and there may be only a single lateral spine on the distal part of the ossicle, or 2-4 lateral spines, also all on the distal part of the ossicle, or there may be 3 (2) distal lateral spines and 1 (2) proximal ones on the projecting lateral corner (fig. 22*c-e*).

A few remarks may be given here about the oral armature in the specimens of *P. irregularis* from the Valdivia st. 63. In the type-specimen the lateral oral spines on some ossicles are very slender, as figured by LIEBERKIND, but on other oralia – as a re-examination has shown – they are shorter and flattened, and so they are also in the two other specimens. The proximal lateral spine may almost assume the appearance of a segmental papilla, and on the ossicle there may be a faint indication of a segmental pit. In the type-specimen of *P. irregularis* one jaw is abnormal in having two unpaired mouth-spines, one above the other, as shown in LIEBERKIND's texfig. 3.

The ventrolateral area is paved with naked plates, partly in a smaller number than in the type of *P. irregularis*, but similarly arranged (cf. LIEBERKIND fig. 1, pl. 3) in indistinct radial rows, two of which about corresponding in width with that of a marginal plate, and with the most distal plates much smaller and more numerous so that about 4 of them adjoin each marginal plate.

In the smallest one of these three large specimens of *Porcellanaster* the arm ends are normal, with the adambulacral furrow ending below the terminal ossicle. In the medium-sized specimen the ambulacral furrow, however, extends up along the distal end of the terminal ossicle (fig. 22*a*, *b*), and in the largest specimen the ambulacral furrow extends on an elongation distinctly below and beyond the terminal ossicle. In four of the arms in this latter specimen the tip is unprotected, apart from some rudimentary plates (fig. 22*l*, *m*), whereas in the fifth arm a denser pavement of plates has been formed around the tip (fig. 22*j*, *k*).

It appears as if the specimens of *Porcellanaster* with a size of R/r about 30-32/9-11 mm and 8-9 superomarginal plates, have reached the full size obtainable by normal growth. (Of the other large specimens of *Porcellanaster* recorded in the literature, LIEBERKIND's *irregularis* with R about 30-33 mm has 8-7 superomarginals, and PERRIER's *granulosus* with R 24 mm has 8-9 superomarginals). Any further growth after such a size is reached becomes then apparently abnormal, as described for the present large specimen.

The specimens from Galathea st. 281, south of Ceylon (fig. 23*d-i*).

These three specimens, which correspond to SLADEN's *Porcellanaster caulifer*, have R/r 21/9 mm, 23/11 mm, and 24/11 mm. The first has an empty stomach, whereas the third has the stomach filled to the utmost, so that the diameter of the disk inclusive of the extremely widened mouth-opening becomes about 28 mm. The superomarginals (fig. 23*h*), 5-6 in number, are mainly subquadrate but sometimes slightly rectangular (in SLADEN's *caulifer* they were distinctly rectangular), and are armed with a fairly large erect dorsal spine; the distal plate possibly is unarmed, and scattered plates may be provided with an additional smaller spine, or with 2 subequal slender spines. The inferomarginals number 6-8, i. e. 1 or sometimes 2 more than the superomarginals. They are about two-thirds as high as the accompanying superomarginals. The cribriform organ may comprise from about 20 up to 34 lamellae. The terminal ossicle is rather globular (in this respect similar to SLADEN's *tuberosus*), in the smallest specimen armed with 3 spines, a distal terminal one and a pair of subterminal ones, and in the other specimens with 5 spines, there being also a proximal dorsal pair of small ones (fig. 23*h*). One ossicle in the large specimen has an extra subterminal spine to one side, and thus 6 spines in all (fig. 23*e*). In the same arm there is further an additional terminal ossicle riding on the antepenultimate superomarginal plate.

The dorsal side centrally and interradially bears spinelets, of which some – especially among those near the margin – are slightly clavate. The scattered perforated plates in the integument radially and in the arms, are slightly larger than the spinelet-bearing ones. All three specimens show a distinct apical appendage. Papulae occur in a broad band interradially. The gonad papillae are observable in some interradii in the smallest specimen.

The subcircular madreporic body is small, its diameter less than the width of the cribriform organ, or about equal to 1/2 or 1/3 of the width of the first inferomarginal plate, and the striae are irregularly arranged. The madreporic body is thus of a peculiar juvenile appearance considering the size of the specimens.

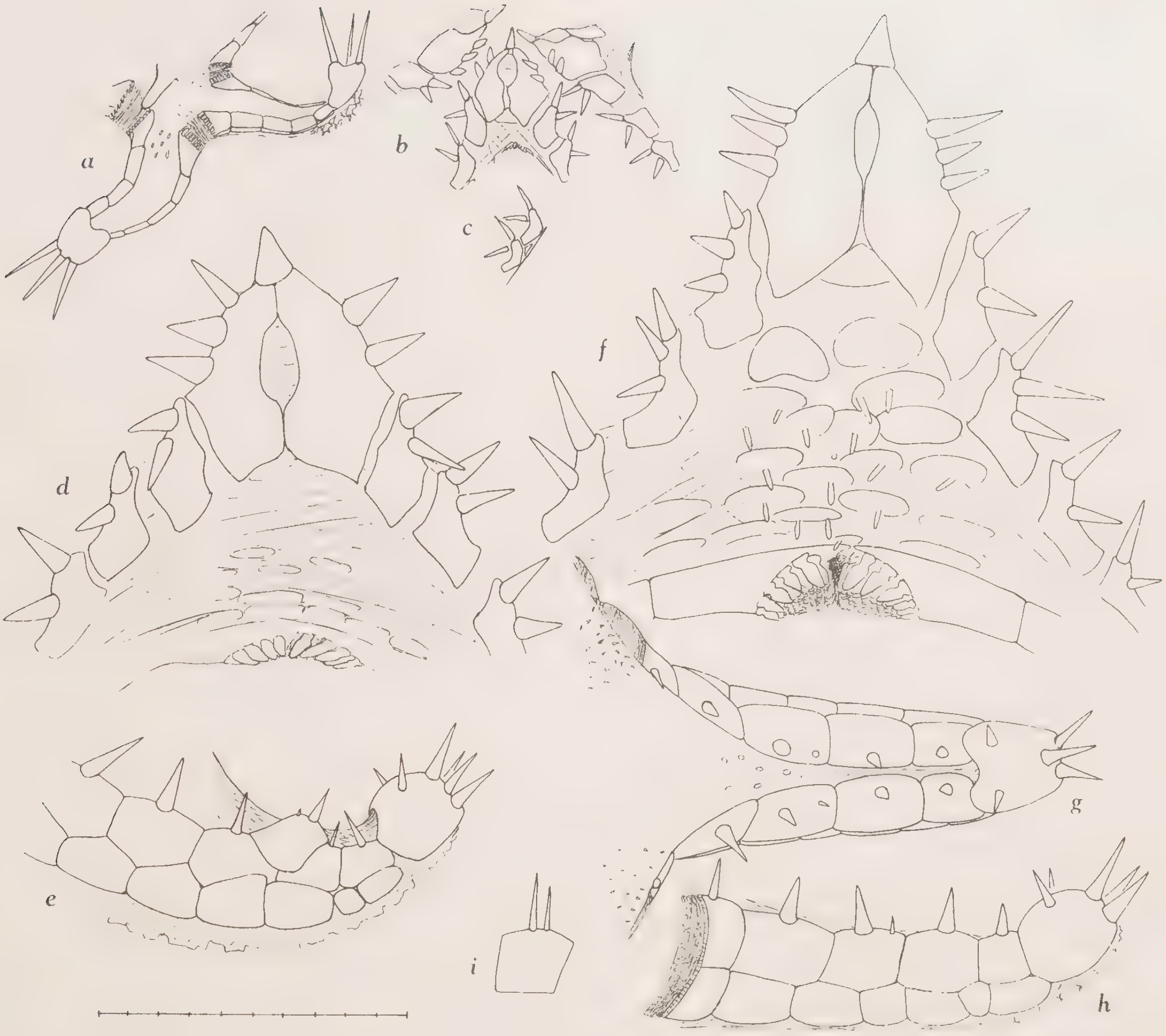

Fig. 23. *Porcellanaster cæruleus.* a-c) St. 282, R/r 7/2 mm; b, part of ventral side; c, adambulacralia nos. 6-7. d) St. 281, R/r 21/9 mm, part of ventral side in twice the usual scale. e) St. 281, R/r 24/11 mm, arm with supplementary terminal ossicle. f-i) St. 281, R/r 23/11 mm; f, part of ventral side in twice the usual scale; g-h, arm in dorsal view and in lateral view; i, superomarginal plate no. 4 in another arm.
Scale: 10 mm (in d and f: 5 mm).

The adambulacral ossicles generally carry 2 spines, but a few of the more proximal ones may bear 3 spines.

The oral armature consists of a stout proximal mouth-spine (one jaw in the larger specimen has 2 proximal mouth-spines, one to each ossicle), and 2-3 lateral spines, slightly longer than the proximal one, and sometimes about as stout, though generally distinctly more slender. The largest specimen has only 2 lateral oral spines, the mediumsized one mainly 3 (fig. 23*f*), and the smallest one 2 and 3 spines about equally common (fig. 23*d*).

The ventrolateral area is provided with a pavement of plates which are all naked in the smaller specimen, whereas a few of those in the larger specimen, and still a few more in the medium-sized one (fig. 23*f*) bear one or two small spines each. About 4 ventrolateral plates adjoin each of the marginal ones. The ends of the ambulacralia may be visible from about the third adambulacral ossicles.

The specimen from Galathea st. 282, south of Ceylon (fig. 23*a-c*).

This juvenile specimen of *Porcellanaster* has R/r 7/2 mm. There are 4-5 superomarginals, rectangular and unarmed, and a corresponding number of inferomarginals. Cribriform organs with about 8 lamellae. Terminal ossicle conspicuous and with 3 long slender glassy spines, a distal terminal one and a pair of subterminal ones. The disk bears in the interradii close to the cribriform organs a number of spinelets, each on its own small plate, and in the integument radially there are scattered small rounded naked plates. There is a long apical appendage. The adambulacralia (12 in number) bear 2 spines. The oralia bear, besides the mouth-spine, 2-3 flattened spines laterally. Ventrolateral plates are not yet developed. The dorsal aspect of the specimen agrees with KOEHLER's fig. 5, pl. 11, 1909*a*; a few spinelets occurring interradially.

The specimen from Galathea st. 63, in the Gulf of Guinea (fig. 24*a-b*).

This juvenile specimen of *Porcellanaster* has R/r about 11/4-5 mm, 5 superomarginals, about twice as long as high, and 5 inferomarginals. The cribriform organ comprises about 18 lamellae. The conspicuous terminal ossicle bears 3, up to 2 mm long glassy spines. The disk is provided with a number of spinelets centrally and interradially, each on its own small plate; radially on the disk and in the arms the integument includes scattered small naked plates. The apical appendage is extended to a length of about 6 mm; its width is about 1/3 mm. The gonad papillae can be distinguished near the sutures between the first and second superomarginals. The madreporite is – as usual in the juvenile specimens – still of a small size in relation to the length of the adjoining marginals. The adambulacralia (15 in all) bear 2 rather long and slender spines, the proximal ossicles sometimes 3 spines. The oral ossicles bear 4 (in one case 3) lateral spines, somewhat shorter and more slender than the fairly stout mouth-spine. The ventrolateral area is provided with a few spaced small (rudimentary) plates with single spinelets. The stone canal is distinctly visible through the integument. In the oral opening are seen the test-fragments of a sea-urchin which, although small, has been large in proportion to the sea-star.

This small specimen corresponds fairly closely to the *Caulaster sladeni* described by PERRIER. It is slightly larger and has correspondingly one superomarginal plate more. (PERRIER also noticed the gonad papillae, though he did not recognize them as such). In the series of North Atlantic specimens from the Ingolf st. 36 listed in the table p. 128, the specimen corresponds to nos. X-XI.

The specimens from Pickle st. 92, near Cape (fig. 24*c-h*).

These two specimens are small, R 8 and 7 mm, and show in ventral aspect a rather different general appearance. The occurrence of two such specimens in the same catch supports the view that all hitherto recorded juvenile specimens of *Porcellanaster* belong to the species *cæruleus*.

The larger specimen with R/r 8/5 mm (fig. 24*c*) has 5 rectangular superomarginals and 5-6 inferomarginals. The cribriform organs are with about 10 lamellae. The terminal ossicles have 3 subequal spines, in one case 4, there being 2 spines side by side instead of the usual unpaired terminal one. Small embryonic plates are discernible dorsally around the long apical appendage, and further there are interradial bands of spinelets, each on its own small plate. Also a few pedicellariae occur interradially on the disk, often 1-2 close to the cribriform organ. The madreporite is of a diameter less than the width of the adjoining cribriform organ, the gonad papillae are well distinct. The adambulacralia, in a number of 10, bear each a pair of spines which form a large pedicellaria (fig. 24*e*), except the two or three distal rudimentary ones, which have only a pair of diverging flattened spines yet. The proximal adambulacral ossicle sometimes has an additional small aciculate spine on the adoral furrow corner, or, which is exceptional in *Porcellanaster* (and may be considered an abnormality), on the ventral surface of the ossicle at the interradial corner (fig. 24*d*). The oral ossicles have, besides a short conical mouth-spine, 3 lateral spines each, a proximal rather spiniform one and 2 flattened ones which as segmental papillae cover a distinct pit on the ossicle. In one case they seem to form a pedicellaria (fig. 24*e*) which when laid down fills out the pit on the ossicle. The ventrolateral area is armed with spaced small plates with spines.

This specimen agrees closely with the description of KOEHLER's *Albatrossaster richardi*, except that it has ventrolateral spinelets, whereas in *richardi* there were only spaced naked plates ventrally.

The other, slightly smaller specimen, with R/r 7/3-4 mm, has also 5 rectangular superomarginals, but still only 4-5 inferomarginals, the series of which do not quite reach to the terminal ossicle. This ossicle bears 3 spines, in one case 4, the distal terminal spine here being reduplicated (fig. 24*h*). The dorsal side is provided with some embryonic plates around the apical appendage and with interradial bands of spinelets, but is without pedicellariae. The gonad papillae are perceptible. The adambulacralia, 9 in number, bear generally 3 long slender and slightly flattened spines along their furrow mar-

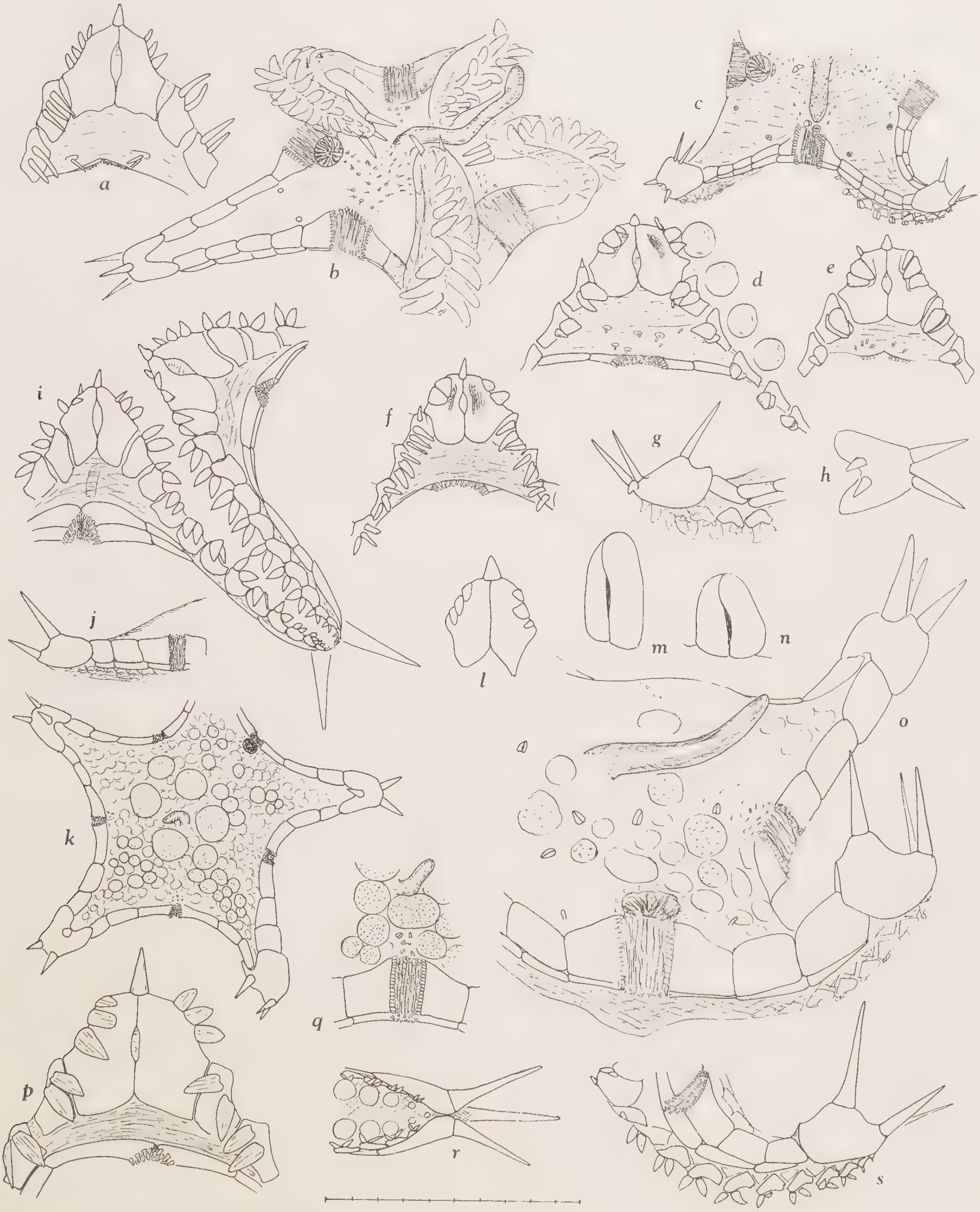

Fig. 24. *Porcellanaster cæruleus.* a-b) Galathea st. 63, R/r 11/4 mm. c-e) Pickle st. 92, R/r 8/5 mm; d-e, two jaws in twice the usual scale. f-h) Pickle st. 92, R/r 7/4 mm; f, part of ventral side in twice the usual scale; g-h, terminal ossicles in twice the usual scale. i-k) Galathea st. 574; i, part of ventral side in twice the usual scale. l) Galathea st. 664, R/r 7/3 mm. m-o) Galathea st. 664, R/r 8/3 mm; m-n, dorsal pedicellariae in four times the usual scale; o, part of dorsal side in twice the usual scale. p-s) Galathea st. 664, R/r 4/2 mm; p, part of ventral side in four times the usual scale; q, part of dorsal side in twice the usual scale; r-s, arm in ventral view and in lateral view respectively, in twice the usual scale.
Scale: 10 mm (in a, d-i, o, and q: 5 mm, in m-n, and p: 2.5 mm).

gin (fig. 24*f*). Two of the proximal ossicles bear 4 furrow spines, and some more distal ossicles may have only two furrow spines. Not a single one of the adambulacralia has its armature formed as a pedicellaria. The oralia carry, besides the conical mouth-spine, 2, or sometimes 3, large flattened lateral spines, which have the appearance of segmental papillae over a segmental pit, or may simulate a pedicellaria. Ventrolateral plates are not yet developed.

The specimen from Galathea st. 574, southwest of Australia (fig. 24*i-k*).

This juvenile *Porcellanaster* has R/r 7/3.5 mm. There are 3 subquadrate superomarginals, slightly longer than high, and 3 inferomarginals about one-third as high as the superomarginals. The cribriform organs, except for that in the interradius with the madreporite, are still rather rudimentary, with only up to 6 lamellae. The conspicuous terminal ossicles carry 3 long spines. The whole dorsal side, also of the arms, still possesses the embryonic plating of rounded perforated plates, those around the apical appendage the largest, five interradial ones here being especially large. Some few spinelets occur near the cribriform organs, each on its own small plate. (A few plates are also found with 2 closely placed spinelets, rudimentary pedicellariae probably). The adambulacralia, 11 in number, each bears a pair of subequal lanceolate flat spines, apparently forming a transitional stage to a veritable pedicellaria. The oralia, besides the short conical mouth-spine, bear 3 subequal, flat pointed lateral spines. Ventrolateral plates are not yet developed.

This specimen agrees perfectly with SLADEN's *P. eremicus* from the South Atlantic west of Cape. Like this it has retained the embryonic plating of the dorsal side at a slightly larger size than hitherto recorded for juvenile North Atlantic specimens of *P. cæruleus,* but otherwise it is indistinguishable from these.

The specimens from Galathea st. 664, in the Kermadec Trench (fig. 24*l-s*).

The three juvenile specimens dredged here range in size from R 4 mm to R 8 mm.

The smallest one, R/r about 4/2 mm, has 3 subquadrate superomarginals and also 3 inferomarginals. Cribriform organs with up to 8 lamellae. Prominent terminal ossicle with 3 long spines. Dorsal side with the embryonic pavement of perforated plates (fig. 24*q*); close to the cribriform organs a few spinelets; also a few dorsal pedicellariae, one of which being merely two close-set spines. Adambulacralia, altogether 10, with 2 subequal, large lanceolate flat spines. Oralia with a fairly long conical mouth-spine and 3 flattened lateral spines (fig. 24*p*). No ventrolateral skeleton.

The medium-sized specimen, R/r 7/3 mm, has 4 superomarginalia, 3 inferomarginalia, and 11 adambulacralia. Cribriform organ with 8 lamellae. Dorsal side with the embryonic plating; no dorsal pedicellariae. The gonad papillae distinct near the sutures between first and second superomarginals. Oral and adambulacral armature as in the smaller specimen, only that the mouth-spine is shorter (fig. 24*l*).

The largest specimen, R/r 8/3 mm (fig. 24*o*), has 3 superomarginalia, 3 inferomarginalia and 11 adambulacralia. Oral and adambulacral armature as in the former specimen. Dorsally in the disk area the embryonic plating is in the state of being absorbed, a few of the perforated embryonic plates are still discernible, but otherwise only some circular markings in the integument indicate their former position and size. In the arms a close covering of plates is still present. Spinelets occur near the cribriform organs, and altogether 10-12 pedicellariae are scattered over the disk. The gonad papillae are discernible. A number of spaced small (rudimentary) plates occur in the ventrolateral areas.

These specimens agree well with SLADEN's *P. eremicus* and also with PERRIER's *Caulaster pedunculatus.*

Distribution:

Porcellanaster sensu stricte, probably a monotypic group: *P. cæruleus,* up to this date has been found in 86 dredgings scattered over all three oceans (fig. 38): 69 dredgings in the Atlantic from south of the Wyville Thomson Ridge to off Cape, eight in the northern Indian Ocean, three in the region of the Malay Archipelago, one in the northern West Pacific, two in the South Pacific, and three in the eastern tropical Pacific. The known bathymetrical range is from 1158 to 6035 m. (Most finds are made between 1600 and 3000 m, 7 (?) between 3000 and 4000 m, 4 between 4000 and 5000 m, 1 between 5000 and 6000 m, and a single one just below 6000 m). The bottom has been blue, green, white, grey, and black mud, globigerina ooze, transition clay, and red clay. The temperatures recorded range from 1.1° to 4.2°C.

Eremicaster Fisher, 1905

Type-species: *Eremicaster tenebrarius* Fisher, 1905 (= *Porcellanaster gracilis* Sladen, 1883).

Diagnosis:

Porcellanasterids with opposite superomarginals separate in whole arm length, and usually armed with dorsal spines. Terminal ossicle distal to arm end, not markedly broader than long. A mid-interradial suture. Three (-5) lamelliform cribriform organs. A single proximal mouth-spine, common to both oralia forming a jaw. Up to six radiating series of ventrolateral plates corresponding with a marginal plate. Lateral oral spines and aboral adambulacral spines sometimes modified as segmental papillae, covering as lids excavated pits on the ventral surface of the ossicles.

Description:

The general appearance of *Eremicaster* and its dorsal armature is like that of *Porcellanaster* (see p. 124). The genus is known to reach a size of R/r about 60/16-20 mm.

The number of cribriform organs may be fairly variable in some porcellanasterids, individually as well as with age, and is, therefore, not immediately acceptable as a generically distinguishing character. But, as discussed p. 125, also some other characters distinguish *Eremicaster* from *Porcellanaster*. Juvenile specimens of *Eremicaster* with yet only a single cribriform organ in each interradius usually may also be recognized by having the ventrolateral skeleton developed at a smaller size than is the case in *Porcellanaster*. Nevertheless, it is possible that some juvenile specimens of these genera may prove indeterminable.

Juvenile specimens of *Eremicaster* up to a size of about R/r 7/3 mm, in general have yet only a single cribriform organ developed in each arm angle, while all specimens on record with R about 8 mm or more, have 3 cribriform organs, at least in the interradius with the madreporite (specimens as large as with R 8-10 mm sometimes having yet only a single cribriform organ developed in the other interradii). Some large specimens of *Eremicaster* collected by the Galathea Expedition have 4-5 cribriform organs in one or more of the interradii.

The jaws bear as a general rule a single spine (the mouth-spine) on their proximal corner, at the junction of the two oral ossicles. But some jaws may be provided (atavistically?) with two proximal spines, one to each oral ossicle, and others even with a group of proximal spines. The number of lateral oral spines is also only small, and normally there are no suboral spines. The adambulacralia likewise bear only a few furrow spines and are normally devoid of any subambulacral armature. (Very exceptionally an oral or an adambulacral ossicle may be found provided with a spine or spinelet on the ventral surface). The lateral oral spines and the adorally placed adambulacral spines on the more proximal ossicles may be transformed into segmental papillae (see p. 42). The superomarginal plates bear usually a single, though sometimes more (up to 4), erect spine(s) on their upper edge. Some specimens, however, are devoid of spines on the superomarginals of the interradial angle, and spines may be totally absent along the whole arm. (The superomarginal spines are not markedly developed in juvenile specimens, and in specimens of the same population they may be present as well as absent). The ventrolateral plates are generally naked, but they may bear spines (e. g. all specimens known of LUDWIG's *E. pacificus*). And also some specimens belonging to species of *Eremicaster* with typically naked ventral plates, have been found provided with a scattered ventral spine-armature. The terminal ossicles in specimens of the same population may bear the usual 3 spines only, or also a great number of spines; and thus the conspicuous appearance of the terminalia in some specimens is of no definite taxonomic importance.

Remarks:

Two of the species described by SLADEN in 1883 in the genus *Porcellanaster*, *crassus* and *gracilis*, were distinguished by having three cribriform organs in each interradius, whereas the others, like the type-species *cæruleus*, had only a single cribriform organ in each arm angle. Further, these two species had part of their oral and adambulacral armature modified in a peculiar way, the spines being flattened, articulated on straight bases running parallel to the furrow, directed outwards from this, and each like a lid covering a pit on the surface of the oral or adambulacral ossicles. SLADEN named this a segmental organ (consisting of a segmental papilla at a segmental pit, see p. 42).

FISHER in 1905 described under the specific name of *tenebrarius* a form related to SLADEN's *crassus* and *gracilis*, likewise with 3 cribriform organs, and with segmental organs developed. He further considered these three forms representing a special subgenus of

Porcellanaster, which he named *Eremicaster,* with the species *tenebrarius* registered as the type.

Ludwig, also in 1905, just a few days later than the appearance of Fisher's paper, published a paper including the description of two new species of *Porcellanaster, pacificus* and *waltharii,* which also had 3 cribriform organs, the first mentioned without segmental organs developed, and the last mentioned with such organs (the latter form proved to be exactly the same as Fisher's *tenebrarius*). In 1907 Ludwig described another related form with 3 cribriform organs but no segmental organs: *vicinus,* and a variety of this form: *vicinus* var. *inermis.* In the same paper he raises *Eremicaster* to the rank of a genus, but uses as type incorrectly Sladen's *crassus* (the first described species in the group) and considers the presence of segmental organs (papillae) the distinguishing character. *Eremicaster* in the sense of Ludwig (1907) thus comprises the following forms, with segmental papillae and 3 cribriform organs: *crassus, gracilis, tenebrarius,* and *waltharii,* whereas the other forms, with 3 cribriform organs but without segmental papillae, viz. *pacificus* and *vicinus,* inclusive of var. *inermis,* were retained in *Porcellanaster.*

Fisher immediately (1907) protested against Ludwig having changed the type of *Eremicaster,* from *tenebrarius* to *crassus;* and further he objected to using the segmental papillae as a taxonomic character, since he had found them in a very varying number in different specimens, the aboral furrow spine being transformed into a flattened lid-like papilla on from as few as 5 to about as many as 15 of the proximal adambulacral ossicles, and the number even varying considerably in specimens from the same catch. The distal part of an arm in a typical specimen of *Eremicaster* has thus always the same kind of adambulacral armature as has the whole arm of a specimen of *Porcellanaster* (with 1 cribriform organ only), and there is then but a slight step to the total disappearance of segmental papillae, for which reason Fisher concluded that it was the presence of 3 cribriform organs in each interradius which was the primary distinguishing taxonomical character. *Eremicaster* in his sense (he now also considers it of generic rank) consequently comprises the following forms: *crassus, gracilis, tenebrarius* (the type-species), *pacificus, waltharii, vicinus,* and *vicinus* var. *inermis.*

Of these *E. waltharii* (as noted by Fisher) is obviously the same as *E. tenebrarius,* which form, however, the present author considers the same species as *E. gracilis. E. pacificus* is a distinct species, and this also applies to *E. vicinus.* (The latter was by the present author formerly believed to be only a form of *E. pacificus* and therefore listed under this name in 1951 and 1956. Its specific validity has been confirmed, however, through the study of the present material).

The Galathea Expedition collected a total of 195 specimens of *Eremicaster* in six dredgings in the Indian Ocean and the tropical Pacific, two of the dredgings – in the Sunda Trench and the Kermadec Trench respectively – undertaken in hadal depths (more than 6000 m). The specimens from the two hadal dredgings belong to *E. vicinus,* and were described preliminarily in 1956, at which time *E. vicinus,* however, as mentioned above, was considered a form of *E. pacificus.* The other specimens of *Eremicaster* collected by the Galathea Expedition in the Indian Ocean, off tropical East Africa and south of Java, and in the eastern Pacific off Costa Rica, appear to represent two forms, which, however, may be only subspecifically different. One of the forms, identical with Sladen's *P. crassus,* is represented by the specimens from the three abyssal dredgings in the Indian Ocean, the other form, identical with Sladen's *P. gracilis,* but in the literature mainly re-

Key to the species of *Eremicaster*

Page

1a. Ventrolateral plates with spines. Terminal ossicle twice as broad as long. Papillae of covering fringe of cribriform organs very large, subquadrate . . . . *pacificus* 160
1b. Ventrolateral plates typically bare (only exceptionally scattered spinelets). Terminal ossicle about as broad as long. Papillae of covering fringe of cribriform organs not especially conspicuous . . 2
2a. A distinct tubular apical appendage, surrounded by small spiniferous plates. So-called segmental organs frequently developed 3
2b. No distinct tubular apical appendage, but possibly an apical cone. Central area of the disk with a pavement of fairly conspicuous plates. So-called segmental organs not developed . . . . . *vicinus* 161
3a. Number of superomarginalia in proportion to that of adambulacralia about 1 : 2 . . . . . . *crassus* 145
3b. Number of superomarginalia in proportion to that of adambulacralia about 2 : 3 . . . . . . *gracilis* 155

corded under the name of *E. tenebrarius*, is represented by the specimens from the dredging in the tropical eastern Pacific.

The two forms, *E. crassus* and *E. gracilis* (= *crassus* subspecies?), mainly differ from each other in the number of superomarginal plates in relation to the size of the specimens, their number being on the average somewhat lower in *crassus* than in *gracilis*, and their size thus correspondingly somewhat larger. The number of adambulacral ossicles in relation to the size of the specimens is the same in the two forms, and the difference between them therefore may best be expressed by the ratio of marginalia to adambulacralia. This ratio in the two forms overlaps however (cf. p. 52), and whereas it is easy to decide to which form a population represented by a fair series of specimens belongs, it may be impossible to do so if only single specimens are available, and these represent the extremes of variation in the particular form. The terminal ossicle is generally more conspicuous in *E. crassus* than in *E. gracilis*, but also this character is very variable. The two forms, *E. crassus* and *E. gracilis*, as far as our present knowledge goes however, certainly appear taxonomically different, but are perhaps best considered zoogeographical subspecies of the same species.

Eremicaster crassus (Sladen, 1883)

Fig. 25-28. Pls. XI-XII.

Porcellanaster crassus n. sp., SLADEN 1883 pp. 225-227; 1889 pp. 141-143, pls. $22_{4\text{-}7}$, $27_{1\text{-}4}$.

Eremicaster tenebrarius, MACAN 1938 pp. 327-329. (Non *E. tenebrarius* Fisher, = *gracilis* Sladen).

SLADEN described his *Porcellanaster crassus* from a single specimen taken by the Challenger in the mid-South Pacific (st. 286: 33°29'S, 133°22'W, 4271 m, red clay, 1.6°C.). It has R/r about 25/10.5 mm (SLADEN's texts of 1889 and 1883 says erroneously 35/10.5 mm); 7 (according to the figures -8) superomarginals, higher than long, and each with an upper erect spine; 9 rectangular inferomarginals; 3 lamelliform cribriform organs. Large, very prominent terminal ossicles, compressed laterally, high tubercular and rounded dorsally, and with 4 spines (SLADEN says that the fourth spine is in the dorsal median line, but really it is placed laterally to one of the sides). Disk area, except arm bases, with a uniform covering of single spinelets; a distinct apical appendage. Adambulacralia with 2 furrow spines, an adoral pointed one, and a median one, which is transformed into a segmental papilla for the greater length of the radius. (Number of adambulacralia 17, judging from the figures). Oralia with 2, as segmental papillae modified lateral marginal spines, besides the single conical mouth-spine. Naked ventrolateral plates.

The drawings of the type-specimen of *Porcellanaster crassus* in the Challenger report seem to agree perfectly with some specimens in the Galathea material, whereas the proportion R/r recorded by SLADEN, and his reference to a median dorsal spine, disagree with them. R/r when measured in the drawings, however, is about 25/10 mm, and thus the 35 mm in SLADEN's text of 1883 might be due to a printer's error, having passed unnoticed into the final edition of his report. Dr. AILSA M. CLARK of the British Museum kindly checked up on this, and confirms that there was an error in the measurement of R as given in the Challenger report. The type-specimen has all the arms curled vertically, and, according to dr. CLARK's re-examination, R is on the dorsal side about 20-21 mm and ventrally 30 mm, giving a mean value of about 25 mm. In the Galathea specimens of *Eremicaster* the armature of the terminal ossicles is very variable, never with a proximal median spine however, but often with one or more dorsal spines proximally to each side of the median line. When seen from the side the spines of such a possible proximal pair might overlap and in a figure appear as a single median spine. Dr. CLARK kindly re-examined also the terminal armature in the type of *crassus* and found, as expected, that the proximal spine was not quite median, being to the left in three cases and to the right in two cases, there being never more than a single proximal spine on any of the terminal ossicles. This arrangement falls well within the variation of the terminal armature in the Galathea specimens from e. g. st. 238, and the present author is thus convinced that these, as well as the specimens from sts. 217 and 474, represent the same species as SLADEN's *Porcellanaster crassus*.

FISHER (1907 and 1911) expressed the opinion that SLADEN's *Porcellanaster gracilis* was merely the juvenile *P. crassus*, but as will be discussed below, the case is not so simple as that. No doubt *P. gracilis* is very closely related to *P. crassus*, and possibly they are only to be considered subspecifically different, but according to our present knowledge they do represent two forms which show constant though rather slight differences. The form of which SLADEN's *P. gracilis* is the first described representative also includes Fisher's new species *E. tenebrarius,* as shown below. Probably, however, not all specimens recorded under the name of *E. tenebrarius* really belong to this form; thus the specimens recorded from the Indian Ocean by Macan in all probability belong to Sladen's *P. crassus,* as will be discussed in the following.

Macan in 1938 recorded and described under the name of *E. tenebrarius* 24 specimens of *Eremicaster* dredged by the Murray Expedition in the northwestern Indian Ocean off Somaliland (st. 171: 9°08'N, 55°30'E, 3840-3872 m), which specimens according to his tabular survey show a slightly lower number of superomarginals in relation to size than is found in the eastern Pacific specimens of *E. tenebrarius* described by Fisher, and, under the name of *P. waltharii,* by Ludwig. This is the principal character by which the form *crassus* is distinguished from the form *gracilis,* as borne out by the study of the specimens available from the Galathea Expedition, and therefore the present author considers it justified to refer these Indian Ocean specimens to *E. crassus.* The Galathea Expedition also collected specimens of *E. crassus* in two neighbouring localities, but did not find *E. gracilis* (= *tenebrarius*) in the region.

Macan's specimens have R/r in mm as follows, with the number of superomarginals added in parentheses: 6/3 (4), 6/3 (5), 7/3 (3), 7/3 (5), 7/3 (5), 7/3 (5), 7/3 (5), 7/3 (5), 8/4 (4), 9/4 (5), 10/4 (5), 10/4 (5), 10/5 (5), 11/5 (5), 15/6 (5), 15/7 (7), 16/7 (6), 16/7 (6), 20/8 (7), 22/8 (8), 23/10 (9), 28/11 (8), 30/10 (11), and 33/12 (12). Macan states that "the specimens agree closely with the description of the American forms", and the correctness of this statement is not disputed, considering the insignificance of the differences by which the two forms are to be recognized. Macan states that the typical number of cribriform organs does not appear till the specimens have reached R 8 mm, and that superomarginal spines in general do not appear till they have reached R 10 mm, and may be wanting on the interbrachial plates in specimens up to R 16 mm. The small specimens have 3 terminal spines, the larger ones 5.

The Galathea material:

A total of 100 specimens of *Eremicaster* referable to Sladen's species *crassus* were collected in three dredgings in the Indian Ocean, viz. in the western part, in the Mozambique Channel and off Kenya respectively, and in the eastern part south of Java.

St. 217: 14°20'S, 45°09'E, 3390 m, 1.6°C., globigerina ooze. 64 specimens.
St. 238: 3°23'S, 44°04'E, 3960 m, 1.8°C., globigerina ooze. 22 specimens.
St. 474: 9°49'S, 114°13'E, 3840-3810 m, 1.2°C. 14 specimens.

The specimens available from st. 217 range in R/r from 7/3 to 25/10 mm, those from st. 238 from 29/9 to 44/13 mm, and those from st. 474 from 9/4 to 58/14 mm. The three populations represented are treated separately in the following, since the two former samples supplement each other with regard to size, and since the third, from st. 474, includes several specimens without the least indication of so-called segmental organs, i. e. with all the furrow spines, inclusive of the lateral oral spines, distinctly acicular.

The population from st. 217. (Fig. 25. Pl. XI 1-6):

The 64 specimens from st. 217 have R/r in mm as follows, with the number of superomarginals added in parentheses: 7/3 (4-5), 8/3 (5), 8.5/3.5 (6), 9/3 (5), 9/3.5 (5), 10/4 (5), 10/4.5 (5), 11/4 (6), 12/5 (6), 13/4.5 (6), 13.5/4.5 (6), 14/5 (6), 14/5 (7), 14/5 (7), 14/5 (7), 14/5 (7), 15/5 (6), 15/5 (7), 15/5 (7), 16/5 (7.5), 16/5 (7-8), 16/6 (9-10), 17/5 (8), 17/8 (9), 18/6 (7), 18/6 (7), 18/6 (7), 18/6 (8), 18/6 (8), 18/6 (8), 18/6 (8-9), 18/6 (9), 18/7 (8), 18/7 (8), 18/7 (8), 18/8 (9), 19/7 (7), 19/7 (8-9), 19/7 (9), 19/7 (9), 19.5/7 (8), 20/6 (8), 20/6.5 (8), 20/7 (7-8), 20/7 (8), 20/7 (9), 20/7 (9-10), 20/8 (7), 21/6 (9), 21/7 (8), 21/7 (9), 21/8 (8), 22/7 (8-9), 22/7 (9), 22/8 (9), 22/9 (8-9), 22/9 (9-10), 23/6 (10), 23/7 (9), 23/7 (9), 23/8 (8), 24/9 (9-10), 24/9 (9-10), and 25/10 (9-10) mm.

The ratio R/r ranges in these specimens from 2.3 (exceptionally 2.1) to 3.3 (exceptionally 3.5), being $\leqq 3$ in all specimens with R 7-16 mm, but occassionally also < 3 in specimens with r up to 2.5 mm, and > 3 only in specimens with R 20 mm or more.

The number of superomarginal plates in relation to the size of the specimens is as follows:

R in mm	Number of superomarginals
7	4-5
8-10	5
8.5-14	6
14-16	7
16-23	8
17-25	9
20-25	10

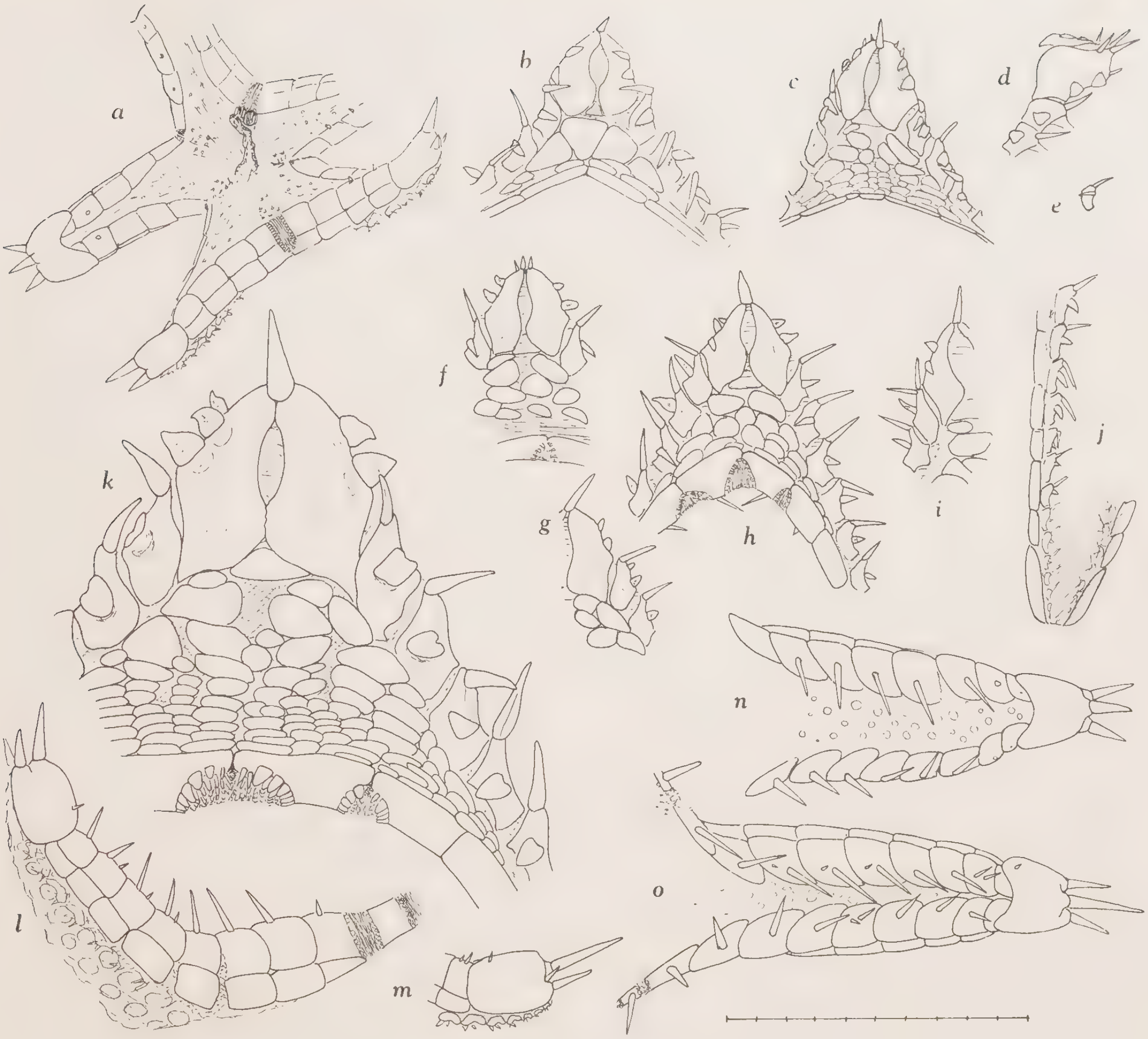

Fig. 25. *Eremicaster crassus.* St. 217. a-b) R/r 7/3 mm; b, part of ventral side in twice the usual scale. c) R/r 19/7 mm. d-e) R/r 20/7 mm, oral ossicle and proximal adambulacralia seen obliquely from the side, and adambulacral ossicle no. 12. f-j) R/r 22/9 mm; f-i, different jaws; j, distal end of arm in ventral view. k-o) R/r 24/9 mm; k, part of ventral side in twice the usual scale; l-o, different arms in different views.
Scale: 10 mm (in b and k: 5 mm).

The interbrachial superomarginal plates are rather subquadrate, and also the proximal superomarginals in the arms are usually subquadrate, though with the upper corners, especially the aboral one, rounded. The same description may apply also to the more distal superomarginals (fig. 25*l*), but often these are subrhomboid with the aboral margin slightly concave and the adoral margin convex (fig. 25*o*). The aboral margin of the superomarginals usually is slightly overlapped by the adoral margin of the following plate (fig. 25*n, o*). In the juvenile specimens with R up to 12 mm, the superomarginals are more rectangular and do not overlap each other distinctly. The inferomarginal plates correspond in number to the superomarginals (perhaps being one or two more distally) and lie nearly always exactly below their superomarginal companions. They are somewhat lower than these, about two-thirds their height, and are rather regularly rectangular.

All the specimens from st. 217 are provided with superomarginal spines, borne on the plates near their dorsal edge. In the juvenile specimen with R/r 7/3 mm (fig. 25*a*; pl. XI 1) the superomarginal spines are still mere granula and present only on the arm plates, whereas the interbrachial plates are still unarmed; and they are rudimentary too in the other small specimens with R up to 11 mm. In all larger specimens the superomarginal spines are well developed. In general there is only a single spine to each plate, erect, slender, spiniform, pointed, and up to about one-third longer than the height of the plate. The spines on the first superomarginals, between the cribriform organs, are often somewhat smaller than those on the second and third plates, and are totally absent in a specimen with R/r 22/9 mm. The following spines are subequal in size almost for the whole length of the arm. Some few (about 10 %) of the specimens are provided with two spines on some plates, exceptionally even three, but then smaller spines.

The number of cribriform organs is still only 1 in each interradius of the juvenile specimens with R/r 7/3 (fig. 25*a*) and 8/3 mm, and also in a few of those with R/r about 9/3 mm. In other specimens with R/r 9/3 to 10/4.5 mm there is in one or more of the interradii a rudimentary cribriform organ present to each side of the median one, consisting at first of only a single row of papillae to the proximal side of the marginal suture. Three cribriform organs become developed first in the interradius with the madreporite. All the specimens with R/r 11/4 mm or more, and 6 or more superomarginal plates, have 3 distinct cribriform organs of a lamelliform structure in each interradius.

The terminal ossicle (fig. 25*l-o*) is distal to the arm end, and slightly larger than this, rather cubic-shaped, with the proximal dorsal margin concave, and with 3-7 spines. Generally there are only the usual three spines on the obtuse distal end of the ossicle, a larger distal terminal one outwards directed above the furrow, and a pair of smaller subterminal ones, one to each side of the end of the furrow and likewise outwards directed. (Exceptionally there are 2 subterminal spines to one or to both sides of the furrow). Some terminal ossicles however, also bear spines or spinelets proximally on their dorsal side, usually a single pair, with one spine to each side (or only one of these spines developed), but occasionally two pairs, with 2 spines to each side of the dorsal mid-line (or 1 and 2). Different terminal ossicles in the same specimen may bear 3 or 5 (4) spines, or 5 and 7 (6) spines. Five terminal spines occur e. g. in a small specimen with R/r 13/4.5 mm, but otherwise the larger number of terminal spines is found mainly in large specimens.

The dorsal side is covered by a fairly thin integument. In the smallest specimen, R/r 7/3 mm, there are in the arms and radially on the disk spaced small rounded perforated plates (the embryonic plates), whereas interradially and mainly near the margin there is a small number of slightly smaller plates, each bearing a single spinelet. This small specimen (fig. 25*a*) has a relatively long apical appendage, with crowded minute plates with minute spinelets. The interradial spine-bearing plates gradually increase in number in the large specimens, and the apical appendage become relatively smaller, being of about the same size in all the specimens, inclusive of the largest ones. The small spine-bearing plates may be fairly crowded, and centrally, around the apical appendage, and near the margin interradially, they may form a close pavement. In the arms, and in the arm bases outside a tangential line connecting the distal corners of the outermost cribriform organs, however, there is always only spaced naked perforated plates of a size of up to 0.3-0.5 mm in diameter, and those of arms on an average slightly larger than those of disk area. Papulae were not perceptible in any of the specimens.

The madreporite is subcircular, with a diameter equal to the width of the first superomarginal plate. It lies close to the marginal plates, sometimes displacing them somewhat, and possibly being almost marginal in position. It is deeply furrowed, and generally with some furrows stretching across in the interradial line of the specimen, whereas the others radiate from the center.

The adambulacral ossicles number about twice as many as the superomarginal plates, as shown by the following examples:

R/r in mm	Number of superomarginalia	Number of adambulacralia
7/3	4-5	10-11
19/7	7-8	15
19/7	7	15
22/9	9-10	20
24/9	9-10	21

The last four, rudimentary adambulacralia are found below the terminal ossicle.

The adambulacral armature typically consists of 2 furrow spines. The adoral one is long (about the length of the ossicle), slender, triangular in section, pointed, and often slightly curved, and is borne on the adoral corner of the ossicle which is protruding somewhat into the furrow. The aboral spine, which is placed medially on the furrow margin, is on the proximal adambulacralia usually transformed into a segmental papilla (a flat subquadrate, subtriangular, or heart-shaped spine), whereas more distally it is rather spiniform, though flattened and always shorter than the adoral spine. Some of the proximal adambulacralia may bear 3 furrow spines, usually 2 spiniform ones adorally, and a single one modified as a segmental papilla aborally, only exceptionally 1 adoral spiniform spine and 2 aboral segmental papillae.

The oral ossicles are typically at their tip provided with the single conical fairly large mouth-spine, common to both ossicles forming the jaw (fig. 25*k*). A single specimen has two mouth-spines to each jaw however, one above the other; and in one specimen a jaw is found with a group of 3 small spines at the tip (fig. 25*f*); and in still another specimen there is a jaw with 4 proximal small spines, 2 to each ossicle (fig. 25*d*). It is possible that such abnormalities have arisen by irregular regeneration of lost mouth-spines. Laterally each oral ossicle is usually provided with two marginal spines in the form of segmental papillae, being broad and flattened and covering a pit on the ossicle. In a few of the specimens it is only the distal marginal spine which has the appearance of a segmental papilla, whereas the proximal one is acicular, and only exceptionally both lateral spines are rather spiniform, not modified as distinct segmental papillae. Some few (about 10 %) of these specimens from st. 217 are provided with an additional third small spiniform oral spine on the proximal lateral corner of the ossicle (fig. 25*d*), deeper in the mouth than the other marginal spines. Some oralia have two such additional spines, thus 4 lateral spines in all. Sometimes only the proximal additional spine is spiniform, whereas the distal one is flattened, there being thus 3 lateral segmental papillae.

The ventrolateral area is provided with a pavement of naked plates. In the small specimen with R/r 7/3 mm, the ventrolateral plates are only few and relatively large, extending as far as to the second inferomarginals (fig. 25*b*), whereas in the largest specimens they are numerous and extend as far as to the fourth inferomarginals. The distal ventrolateral plates, near the marginals, are transversely elongate, small (rudimentary) and arranged in indistinct radiating series, four to six to a marginal plate (fig. 25*k*); the plates near the oralia are much larger and irregularly shaped. In the larger of these specimens from st. 217 there are about 10 indistinct tangential rows of ventrolateral plates, the most proximal row typically with only two plates, the second row with four somewhat smaller plates, and then outwards a gradually increasing number of still smaller plates.

The population from st. 238. (Figs. 26 and 27. Pl. XI 7-12):

The 22 specimens of *Eremicaster* available from this station have R/r in mm as follows, with the number of superomarginals added in parentheses. 30/10 (10), 32/11 (10), 34/12 (11), 34/13 (11), 35/11 (10), 35/11 (10), 36/12 (11-12), 37/11 (10-11), 37/11 (11-12), 37/13 (13), 37/13 (13), 38/10 (12-13), 38/11 (11-12), 39/11 (12-15), 39/13 (12-13), 40/11 (14-15), 40/13 (13-14), 41/13 (14), 42/12 (13-14 (-15-16)), 43/12 (13), 43/13 (14-15 (-16-17)), 43/14 (11-12).

These specimens are thus somewhat larger than those described from st. 217, and supplement these in the survey of the variation and change in the characters with growth. With increasing size also the range of variation in number of superomarginals increases. The specimen with R/r 39/11 mm has 12 superomarginals in a regular sequence in four arms, but 15 are present in one arm. The largest specimen, R/r 43/14 mm, has a regular sequence of only 11-12 superomarginal plates, whereas another of about the same size, R/r 43/13 mm, has 14-15 superomarginals in regular sequences, and, in addition, a few extra ones inserted distally in some of the arms, but not reaching to the inferomarginals (fig. 26*k*). The same also applies to a specimen with R/r 42/12 mm.

All the specimens from st. 238 have, in accordance with their fairly large size, well developed superomarginal spines, usually tapering spiniform (fig. 26*a*), but occasionally somewhat flattened and spearhead-shaped (fig. 26*h, i*). All the specimens have also at least some superomarginals provided with 2 or sometimes 3 spines, exceptionally even 4 spines. In some specimens nearly all superomarginals bear 2-3 spines, i. e., either two about subequal ones, or a medially placed one with a smaller somewhat diverging one to each side. The spines on the first superomarginals are often smaller than the others.

The cribriform organs number 3 in each interradius in all the specimens. Only one specimen, R/r 31/13 mm, shows a slight irregularity in one of the interradii, in which to one side there are three superomarginal plates corresponding with two inferomarginal ones. Cribriform organs are here developed around each of the two superomarginal vertical sutures, which correspond to a single inferomarginal one, and so there in this arm angle are 4 cribriform organs on the series of superomarginal plates.

The terminal ossicle may bear 3 spines only,

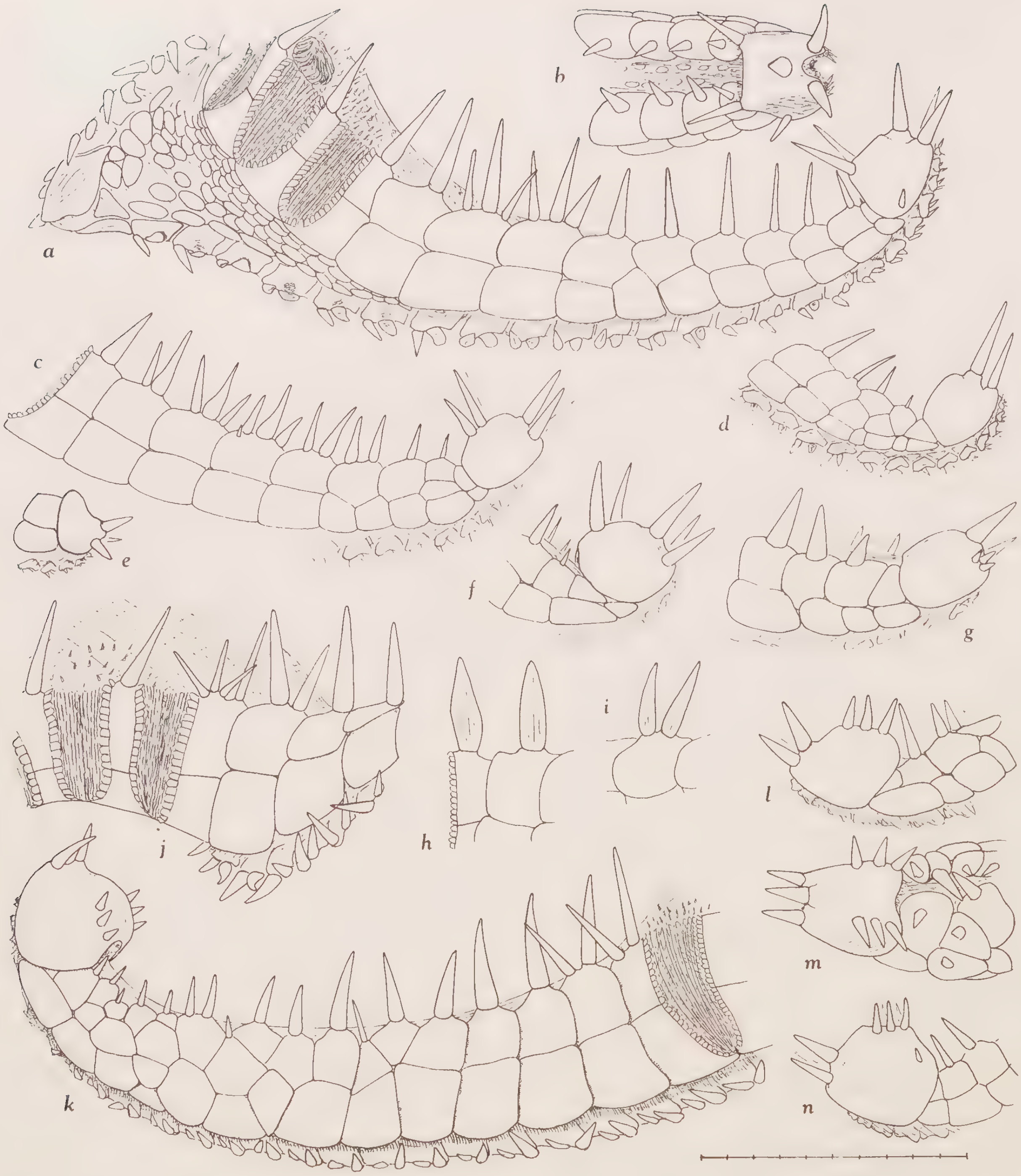

Fig. 26. *Eremicaster crassus.* St. 238. a-b) R/r 36/11 mm, same arm. c) R/r 30/10 mm (see also fig. 27 m.n). d) R/r 37/13 mm. e) R/r 42/12 mm, abnormal terminal ossicle, (see also fig. 27 o-p). f) R/r 37/11 mm (see also fig. 27 c-d). g) R/r 43/12 mm. h-i) R/r 41/13 mm, superomarginals nos. 2-3 and 6 respectively. j-n) R/r ab. 43/13 mm; j, arm angle; k, arm in lateral view; l-m, distal end of another arm in lateral view and in dorsal view; n, distal end of a third arm in lateral view. Scale: 10 mm.

thus e. g. in the specimen with R/r 37/13 mm (fig. 26*d*). Usually, however, the terminal ossicles are provided with an additional pair of spinelets on their proximal surface (as was also the case in some of the specimens from st. 217), and there may be up to three pairs of proximal dorsal spines, as e. g. in a specimen with R/r 43/13 mm (fig. 26*k, n*). The terminal ossicle may further bear a spine or spinelet on its lateral side near the lower margin, as e. g. in a specimen with R/r 36/11 mm (fig. 26*a*), or closer to the upper lateral margin, as in the specimen with R/r 43/13 mm. Thus a single terminal ossicle may be provided with as many as 11 spines. Also the subterminal spines may, though rarely, be reduplicated. Often the terminal ossicles of the same specimen bear different numbers of spinelets, 3-4 or 5-more. In the preserved specimens the terminal spines are frequently lost or broken. Perhaps they are also easily damaged in life. A few terminal ossicles have only a small distal spinelet, and then it possibly is in regeneration. As mentioned above, it seems that when the tissue has been damaged, a group of minute spines may develop instead of the usual large single one.

The appearance of some of the terminal ossicles in these specimens from st. 238 is exactly the same as in the specimens from st. 217, but others are much more swollen and conspicuous in relation to the size of the arms. Such specimens agree closely with SLADEN's type-specimen of *P. crassus*, which has convinced the present author that all these specimens from st. 238 as well as those from st. 217, are representatives of this species. Generally the terminal ossicle is longer than high, but occasionally the reverse is the case, as in a specimen with R/r 37/11 mm (fig. 26*f*).

The dorsal armature shows no variation from that described for the larger of the specimens from st. 217. Papulae however, were to be seen in a few of the large specimens, scattered between the interradial spinelets, and of about the same size as the basal plates of these. An apical appendage is present in all the specimens. In one specimen, R/r 59/13 mm, the gonad papillae were discernible close to the distal corner of the first superomarginal plate.

The adambulacralia number about twice as many as the superomarginalia, and this is the case in all specimens, from the smallest to the largest ones present, e. g.

R/r in mm	Number of superomarginalia	Number of adambulacralia
30/10	10	21-22
30/11	11-12	25
37/13	13	26
37/13	9-11	20-21
42/12	13-14	29-30
43/13	16-17	30
43/14	11-12	23-25

The adambulacral armature may be exactly as described for the specimens from st. 217, consisting of two spines of which the adoral one on the protruding corner of the ossicle is fairly long spiniform (perhaps triangular in cross-section) pointed and often slightly curved, whereas the aboral one (on the more proximal adambulacralia) is modified as a distinct segmental papilla, hollowed out, and usually with a rounded end, as shown in fig. 27*j, p, s*. In one specimen, however, it is very broad, square-shaped and with a peculiarly dented outer margin (fig. 27*d*), and in others it has the end more or less drawn out, and is then rather hook-shaped (fig. 27*u*), and thus can hardly be designated as a segmental papilla. In the latter cases also the adoral spine may be broad flattened and more or less hook-shaped. Segmental pits are distinct on the adambulacralia of some specimens, but are in others hardly – if at all – discernible. In most of these specimens from st. 238, the aboral furrow spine though broad and flattened, is not at all formed as a segmental papilla. And it may be a slender though flattened spine. Three adambulacral spines occur exceptionally on scattered ossicles, and then it is always the adoral spine which is reduplicated (fig. 27*c*). In a single specimen, R/r 30/10 mm, some of the distal adambulacralia were found to be provided with a small spinelet on their surface.

The oral armature shows about the same variation as described for the specimens from st. 217. The usual single mouth-spine may be replaced by 2 spines, one to each oral ossicle, or by a group of small spinelets to each oral ossicle (fig. 27*s*). In the same specimens, however, there are also jaws with the usual single conical spine at the tip. The two lateral oral spines are subequal to the aboral furrow spines of the proximal adambulacralia, and thus in general modified as segmental papillae, flattened and somewhat hollowed, and with either a pointed or a rounded distal end. Occasionally the end of the oral papillae is drawn out into a curved slender tip, giving the papillae a shape like a hook, or the papillae are very broad (square-shaped) and have the distal end dentate. The segmental papillae generally fit into a segmental pit on the ossicle, but such a pit is not always discernible. Also a few specimens in this population have a third lateral oral spine, proximally to the usual two, somewhat deeper in the mouth, generally spiniform (fig. 27*h*), but sometimes modified as a third segmental papilla. Exceptionally all the lateral oral spines are spiniform, and this may be the case also in specimens with adambulacral segmental papillae. A single oral ossicle in a specimen with R/r 39/13 mm bears on its surface, midway between the lateral squamiform spines and the suture, a small spiniform spine, and

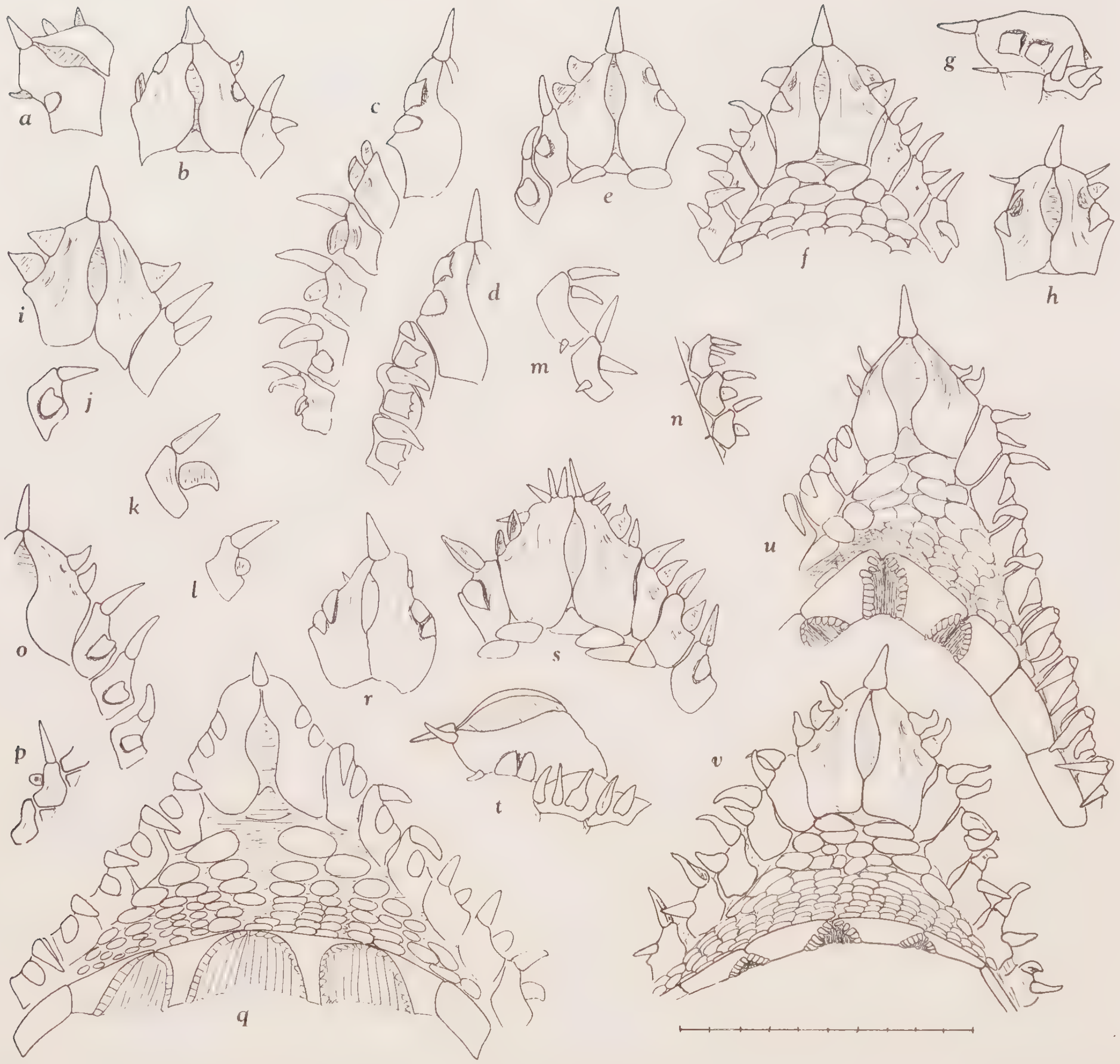

Fig. 27. *Eremicaster crassus*. St. 238. a-b) R/r 32/11 mm, two jaws in different views. c-d) R/r 37/11 mm (see also fig. 26 f). e) R/r 36/11 mm. f-h) R/r 37/13 mm; g-h, same jaw in lateral view and in ventral view. i-j) R/r 36/12 mm, j, adambulacral ossicle no. 4. k) R/r 43/13 mm, adambulacral ossicle no. 4. l) R/r 34/13 mm, adambulacral ossicle no. 5. m-n) R/r 30/10 mm; m, adambulacralia nos. 15-16, in twice the usual scale; n; adambulacralia nos. 12-14, (see also fig. 26 c). o-p) R/r 42/12 mm; p, adambulacral ossicle no. 14. q-t) R/r 41/13 mm, different jaws. u-v) R/r 40-44/12-13 mm, different jaws. Scale: 10 mm (in m: 5 mm).

this is the only case hitherto recorded of a suboral spine in the group of *Eremicaster*.

The ventrolateral area is as described for the specimens from st. 217.

The population from st. 474. (Fig. 28. Pl. XII).

The 14 specimens of *Eremicaster crassus* represented from this station range in size from a juvenile to one almost as large as any one on record. They have R/r in mm as follows, with the number of superomarginals added in parantheses: 9/4 (5), 14/5.5 (6), 18/6 (6), 22/6.5 (7), 29/7 (9), 31/11 (9), 31/11 (10), 34/9.5 (10), 35/11 (12 (-13)), 36/10 (10-11), 37/11 (10), 37/14 (12-14), 43/12.5 (13-14), 58/14 (15-16).

The ratio R/r ranges from 2.2 by R 9 mm to 4.1 by R 58 mm, but may be 4.1 also in a specimen with R only 9 mm, and 2.7 in a specimen as large as with R 37 mm. The superomarginal plates are regularly arranged in all the specimens. The inferomarginal ones generally lie exactly below their superomarginal companions for the greater length of the arms, but are distally often present in a number of 1-2 more. They number e. g. 8 in the specimen with R/r 18/6 mm and 6 superomarginals, and 15-16 in

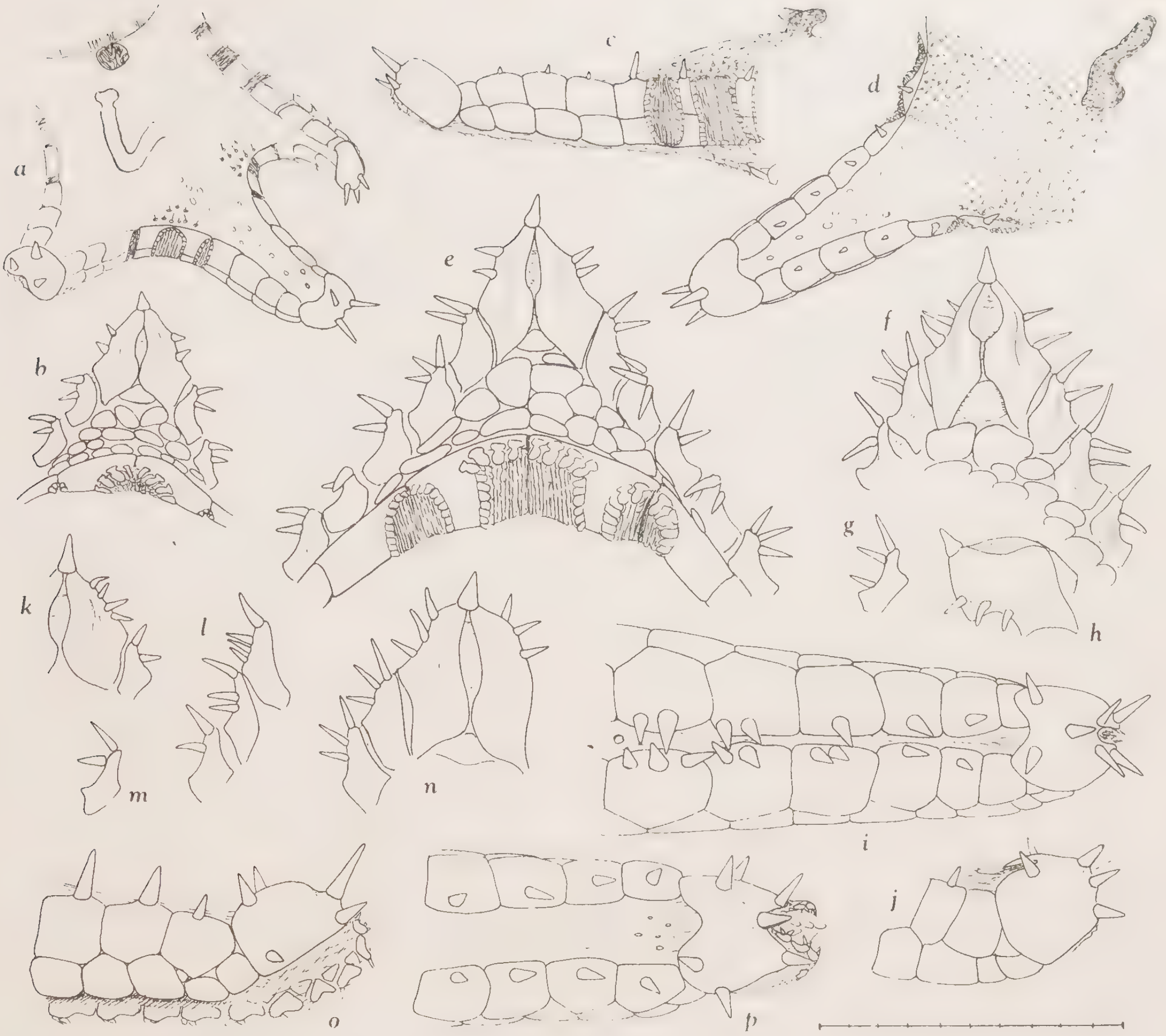

Fig. 28. *Eremicaster crassus.* St. 474. a-b) R/r 9/4 mm; b, part of ventral side in twice the usual scale. c-e) R/r 14/5.5 mm; e, part of ventral side in twice the usual scale. f-j) R/r 34/9.5 mm; g, adambulacral ossicle no. 3; i-j, arm in dorsal view and in lateral view. k) R/r 29/7 mm. l-p) R/r 37/11 mm; l-m, adambulacralia nos. 1-3 and 5 respectively; o-p, distal part of arm in lateral view and in dorsal view.
Scale: 10 mm (in b and e: 5 mm).

that with R/r 43/12.5 mm and 13-14 superomarginals, but also 15-16 in that with R/r 58/14 mm and 15-16 superomarginals, and only 11 in one with R/r 35/11 mm and 12 superomarginals.

In the present population, the juvenile specimen with R/r 9/4 mm (fig. 28*a*) still has no superomarginal spines developed. The other small one, R/r 14/5.5 mm (fig. 28*c, d*), has spines on all the superomarginals except the distalmost ones, but only those on the first and second superomarginals are well developed, the others are all yet rudimentary. As in the two other populations described, each superomarginal plate is usually provided with a single spine only, but in some specimens a varying number of the superomarginal plates carry 2 or 3 spines (in the usual longitudinal row), and in the specimen with R/r 43/12.5 mm there may be up to 5 and then more irregularly arranged spines on the more distal superomarginals. On the first superomarginals the spines may be only small, and in some cases apparently not developed at all, as e. g. in the specimen with R/r 37/11 mm.

The number of cribriform organs is 3 in each interradius already in the juvenile specimen, and it is also 3 in all the other specimens up to a size of R/r 43/12.5 mm; but in the single, very large specimen, with R/r 58/14 mm (pl. XII 8), there are 5 cribriform organs in each interradius. While the three median cribriform organs are of the usual lamelliform structure, the supplementary outermost ones are rather papilliform. They are composed of up to 8 rows of papillae and are thus, though narrow, well marked.

The terminal ossicles in these specimens from south of Java are less conspicuous than in those from sts. 217 and 238 in the western part of the Indian Ocean. Four specimens, the three smallest and one with R/r 29/7 mm, have only the three typical terminal spines, whereas one with R/r 22/6.5 mm, and also all the remaining larger specimens, have at least 5 terminal spines, there being an additional proximal pair dorsally, with one spine to each side, or two pairs of dorsal spines proximally, and in a few cases further a small spine laterally to each side near the margin, adjacent to the inferomarginal plates, thus 7 spines in all (fig. 28*p*). In a specimen with R/r 34/9.5 mm there is also an extra pair of subterminal spines, and the terminal ossicles in this specimen thus bear 7 or 9 spines in all, depending on whether they are provided with one or two pairs of proximal dorsal spines (fig. 28*i,j*).

The dorsal armature in these specimens, except the smallest one, shows the same variation as described for the specimens from sts. 217 and 238, with the spinelets increasing in number with growth, but never spreading beyond the distal corner of the outermost cribriform organs, and with the arm bases and the arms provided only with spaced naked plates, which in some of the large specimens may reach a size of about 1 mm in diameter, but in other equal-sized specimens are at most 0.5 mm in diameter. All specimens have a distinct apical appendage. The juvenile specimen with R/r 9/4 mm shows radially on the disk fairly large circular spots, which may be interpreted as indicating the places of the embryonic plates, which, however, are now absorbed. In this specimen the dorsal spinelets are also still confined to the interradial area, near the margin. Two of the medium-sized specimens show papulae scattered over the main disk area. The specimen with R/r 37/11 mm has the gonad papillae observable in some interradii.

The adambulacral and oral armature is in about one-third of these specimens from st. 474 similar to what was described for the specimens from sts. 217 and 238 (i. e. with the aboral adambulacral spines and the lateral oral ones transformed into segmental papillae). The adambulacral segmental papillae are usually subcircular, but in one specimen they are very broad and with the distal squarely cut margin dentate. Segmental papillae may be found developed on the adambulacralia for almost the whole length of the arm. In about two-thirds of the specimens from st. 474 however, all adambulacral spines, and also the lateral oral ones, are acicular (fig. 28*b, e, f, n*), there being thus no so-called segmental organs formed at all. Usually there are only two adambulacral spines placed close together and diverging on the protruding adoral part of the furrow margin, but 3 spines to each adambulacral ossicle (especially of the more proximal ones) is more frequently occurring when the whole armature is spiniform, than when the aboral spine is modified as a segmental papilla (which also occupies more space on the ossicles than do the spiniform spines). A single specimen, R/r 37/11 mm, bears 4 spines on one of the first adambulacral ossicles. The number of adambulacral ossicles is e. g.:

R	Number of superomarginalia	Number of adambulacralia
9 mm	5	11
14 mm	6	14-15
34 mm	10	20
35 mm	12	21
43 mm	13-14	26
58 mm	15-16	30

In the specimen with R/r 37/11 mm the ambulacral furrow reaches just beyond the terminal ossicle.

The oral ossicles may show, at the tip of the combined pairs, only a minute spine, instead of the usual fairly large conical mouth-spine, or there may be two such minute spines, one on each ossicle. Proximally to the usual lateral oral spines, an additional slender spinelet may occur on the lateral corner of the ossicle. There are usually two lateral oral spines, but a few specimens have 3 spiniform spines laterally, at least on some of the oral ossicles, and a single specimen has 4 lateral spiniform spines on one of the oralia (on the others 3). A single oral ossicle is seen with only one lateral spine (in this case modified as a segmental papilla).

The ventrolateral plates are naked. The number of tangential rows e. g. is 6-7 in the specimen with R/r 43/12.5 mm.

Biological remarks:

One of the large specimens from st. 217 was found with female gonads which though almost emptied still contained a few eggs about 0.5 mm in diameter.

A dendrogate ascothoracid with nauplii larvae was found in a specimen with R about 40 mm.

Distribution:

Eremicaster crassus is known, besides from the type-locality in the mid-South Pacific, from four dredgings in the Indian Ocean: three off tropical East Africa and one south of Java (fig. 39). It has been found at depths from 3390 to 4271 m, on a bottom of red clay and globigerina ooze, and at temperatures of 1.2°-1.8° C. (In the eastern Pacific it is represented by a closely related form, *E. gracilis*).

Eremicaster gracilis (Sladen, 1883)

(E. crassus subspecies).

Fig. 29. Pl. XIII, 1-2.

Porcellanaster gracilis n. sp., SLADEN 1883 pp. 227-229; 1889 pp. 143-145, pls. 22_{1-3}, 27_{5-8}.
Porcellanaster (Eremicaster) tenebrarius n. sp., FISHER 1905 (10/6) pp. 293-294.
Porcellanaster waltharii n. sp., LUDWIG 1905 (17/6) pp. 92-97, pl. 5_{26-27}.
Eremicaster tenebrarius, FISHER 1911 pp. 24-29, pls. 1_{1-4}, 2_{4}, 53_{4-4a}.
Eremicaster tenebrarius, H. L. CLARK 1913 p. 187.
Eremicaster tenebrarius, H. L. CLARK 1920 pp. 76-77.
Eremicaster tenebrarius, DJAKONOV 1950 p. 21, fig. 31.
Eremicaster tenebrarius, ANDRIJASCHEV 1952 p. 134.
Non: *Eremicaster tenebrarius,* MACAN 1938 *(= E. crassus).*

SLADEN described his species *Porcellanaster gracilis* on the basis of a specimen taken by the Challenger in the South Pacific off Chile (st. 298: 34°07′S, 73°56′W, 4070 m, blue mud, 1.3° C.). R/r 10/4.5 mm; 8 subquadrangular superomarginal plates, usually with a dorsal spinelet; 3 lamelliform cribriform organs. Terminal ossicle fairly inconspicuous, with 3 spines. Dorsal side with spinelets in interradial bands; papulae present; a distinct apical appendage. Adambulacralia with 2 spines, the aboral one transformed into a segmental papilla on the proximal ossicles (the number of adambulacralia 13, judging from the figure). Oralia, besides the mouth-spine, with 2 as segmental papillae modified lateral spines. Naked ventrolateral plates.

It is evident that SLADEN's *P. gracilis* is closely related to his *P. crassus*. FISHER (1907, 1911 p. 28) in connection with his discussion of the relationships of his own species *E. tenebrarius,* also suggests that *P. gracilis* is probably only a very young specimen of *P. crassus* "because the differences cited are such as would be expected in a young example". But when FISHER's own form *E. tenebrarius* is included in the considerations one may wonder, however, why he should connect *gracilis* with *crassus,* and not with his own *tenebrarius.* It is really impossible to point out any taxonomical characters distinguishing *gracilis* from *tenebrarius,* and the features which FISHER mentions as distinguishing his *tenebrarius* from *crassus* (primarily a greater number of superomarginals) are the same by which *gracilis* differs from *crassus.* Therefore the present author must conclude that FISHER's *E. tenebrarius* is identical with the form previously described by SLADEN under the name of *P. gracilis.* But, as has been pointed out above (cf. also p. 145), this form differs only slightly from *crassus,* and perhaps is best regarded only as a zoogeographical subspecies (if to be kept distinct at all).

FISHER (1905) described his *Porcellanaster (Eremicaster) tenebrarius* on the basis of three specimens dredged by the Albatross off California (st. 4397: 200 miles off San Diego, 4016-4075 m, gray mud), and a few days later LUDWIG published, under the name of *Porcellanaster waltharii,* a description of the same form based on 30 specimens collected by the Albatross in eight dredgings somewhat farther south, in the Panamic region (st. 3360: 6°17′N, 82°05′W, 3058 m, fine black and green sand, 2.4° C.; st. 3361: 6°10′N, 83°06′W, 2690 m, green ooze, 2.6° C.; st. 3374: 2°35′N, 83°53′W, 3334 m, green ooze, 2.4° C.; st. 3381: 4°56′N, 80°53′W, 3241 m, green mud, 2.1° C.; st. 3399: 1°07′N, 81°04′W, 3182 m, green ooze, 2.2° C.; st. 3400: 0°36′S, 86°46′W, 2418 m, globigerina ooze, 2.2° C.; st. 3414: 10°14′N, 96°28′W, 4082 m, green mud, 2.1° C.; and st. 3415: 14°46′N, 98°40′W, 3436 m, globigerina ooze, 2.2° C.).

That *P. waltharii* is the same as *E. tenebrarius* is noted by FISHER in 1907 p. 12. In 1911 FISHER, besides repeating the description (slightly emended) of the three original specimens of *E. tenebrarius,* described three additional specimens from a neighbouring locality (Albatross st. 4394: 200 miles off San Diego, 4132 m, gray mud), and 45 specimens from an Albatross dredging off southern Alaska (st. 2859: off Prince of Wales Island, 2870 m, gray ooze, 1.6° C.).

H. L. CLARK in 1913 records a single *E. tenebrarius* from off Lower California (Albatross st. 5684: S. W. of Santa Margarita Island, 3219 m), and in 1920 he records 24 specimens from five Albatross dredgings in the eastern tropical Pacific off Peru (st. 4647:

4°33′S, 87°43′W, 3667 m, globigerina ooze, 1.9°C.; st. 4658: 8°30′S, 85°36′W, 4335 m, green mud, 1.8°C.; st. 4666: 11°56′S, 84°20′W, 4755 m, gray ooze, 1.6°C.; st. 4672: 13°11′S, 78°18′W, 5204 m, diatom ooze, 1.8°C.; and st. 4717: 5°11′S, 98°56′W, 3938 m, red clay, globigerina ooze, 1.8°C.).

In 1950 Djakonov recorded *Eremicaster tenebrarius* from east of Kamchatka, 4200 m. (In 1938 Macan recorded and briefly described, under the name of *E. tenebrarius,* 24 specimens dredged by the Murray Expedition in the northwestern Indian Ocean, but, as demonstrated above, these are in reality representatives of *E. crassus).*

The type-specimen of Fisher's *E. tenebrarius* has R/r 37/12 mm (Fisher 1905) and 15 superomarginals (judging from the photo published by Fisher 1911 pl. 1, 1). In 1911 Fisher gives the size of two other Californian specimens as R/r 38/11 and 42/9 mm, and records the number of superomarginals as from 15 to 18-19 in large specimens. The single Californian specimen recorded by H. L. Clark (1913) had R/r 25/8 mm and 10 superomarginals. Twenty of the specimens described from the Panamic region by Ludwig in 1905 (under the name *waltharii)* had R/r in mm as follows, with the number of superomarginals added in parentheses: 10/4 (7), 12/5 (7), 13/6 (8), 14/5.5 (8), 17/7 (8), 18/7 (8), 24/8 (10), 28/9.5 (10), 31/11 (12), 32/11 (14), 36/13 (13), 38/12 (15), 41/15 (15), 43/13 (16), 46/14 (14), 48/15 (16), 50/15 (15), 54/16 (16), 56/17 (16), and 60/16 (20). Ludwig also notes that 8 adambulacralia correspond to 6 marginalia in the median part of the arms of large specimens. One of the Alaskan specimens, which Fisher discusses in 1911, has R/r 22/6 mm, others R/r about 22/8 mm, and 12 or (judging from the photo pl. 1, 3) 11 superomarginals, and a small one has R/r 10/5 mm and 8 superomarginals. Fisher states that the number of superomarginal plates in this Alaskan material is up to 17, but does not say how large the specimens are. The Peruvian specimens recorded by H. L. Clark (1920) had R up to 45 mm.

The characters of *E. tenebrarius,* according to Fisher's descriptions, are as follows: Superomarginals subquadrate, typically with an erect spine on their upper edge, sometimes 2 or even 3 spines, or no spines at all (as in 33 of the 45 specimens from the single Alaskan dredging, which, however, are probably all young ones with R/r from 10/5 to on an average 22/8 mm?). Inferomarginals lower than superomarginals. Terminal ossicle as large as two last superomarginals, strongly concave proximally, in the type-specimen with 5 spines, a distal terminal one, a pair of subterminal ones, and one to each side dorsally. (In the Alaskan specimens recorded, and in juveniles from the Panamic region, only 3 terminal spines). Dorsal side with small rounded plates, those of disk with single spinelets. A distinct apical appendage. Papulae in disk area. Adambulacralia with 2 (proximally perhaps 3) furrow spines, the aboral one transformed into a segmental papilla (in the type for some length of the inner half of the arms, in other specimens for almost the whole length of the arms, and in an Alaskan specimen with R/r 10/5 mm only on the two or three most proximal adambulacralia). Oral ossicles, besides the mouth-spine, with 3 lateral oral spines, the proximal one a slender, curved spinelet, the two others transformed into segmental papillae. (Other specimens have only the two segmental papillae laterally on the oralia). Ventrolateral area with naked elliptical plates. (Number of superomarginalia in relation to that of adambulacralia, according to Ludwig, e. g. 3/4).

The Galathea material:

A large number of specimens of *Eremicaster* referable to the form *gracilis* (syn. *tenebrarius)* were collected in a dredging off Costa Rica, in the region of the eastern tropical Pacific from where the form has been recorded repeatedly previously. They were of a whitish colour with the filled stomach showing greyish blue through the integument.

St. 716: 9°23′N, 89°32′W, 3590 m, 2.0°C., dark muddish clay. 86 specimens.

The specimens range in size from R/r about 8/4 to about 57/16 mm, and thus the series includes specimens as small as any one hitherto recorded as well as specimens of about the known maximum size. The size of the individual specimens and their number of superomarginal plates, for some also the number of adambulacral ossicles, are recorded in the following survey. Part of the material is in a rather poor state, so sometimes the length of r could not be stated. (Incidentally, the figures of r should always be regarded with some caution, especially in the small specimens, since it can never be measured exactly).

R/r in mm	Number of superomarginalia	Number of adambulacralia
8-9/4	8-9	–
13/4.5	8	13
14/?	–	–
14/5	9	13-14

R/r in mm	Number of superomarginalia	Number of adambulacralia
15/?	–	–
15/?	–	–
16/6	9	15-16
17/?	–	–
17/?	9	–
18/?	–	–
18/?	–	–
18/?	–	–
18/?	10	–
18/6	10	–
18/7	9	17
19/?	–	–
19/?	–	–
20/?	–	–
20/?	12	–
20/6	10	14
20/7	10	–
21/8	10-11	17
22/?	-	–
22/6	12	17
22/6	12	18
22/7	12	17
26/?	–	–
28/?	–	–
30.5/6.7	14	21
32/10	15-16-17	21
33/9	13	–
33/9	14-16	21
34/11	13	–
35/8	17	23
39/?	15	21
40/10	15	22
42/11	16	24
43/10	19	24
43/11	18	23
43/13	17	24
44/11	16	24
44/11	18	23
44/13	16	25
46/11	18	27
46/11	22	26-27
46/13	17	25
46/15	18	24
47/12	20	26
47/15	17	23
47/15	18-19	25-26
47/15	19	26-27
48/12	18	25
48/12	18	26
48/12	19	24
48/12	19	26
48/13	18	24-25
48/13	20	29
48/13	17-18	25-26
50/11	17	–
50/12	18	27
50/13	20	24-25
50/13	20-21	27
50/14	19	27
50/15	18-19	27
50/16	20	–
51/13	16	26
51/13	17	28
51/13	21	26
51/15	17	26
51/15	18	–
51/15	19	–
52/12	17	–
52/12	19	25
52/12	22	28
52/14	22	27
52/14.5	18	27
52/15	22	27
55/11.5	20	29
55/14	21	27
55/15	19-20	28
55/15	20	27-29
56/15	19-20	28
57/16	21-23	29-30

The number of superomarginal plates in relation to the size of the specimens is as follows:

R in mm	Number of superomarginalia
8-13	8
14-18	9
18-20	10
21	11
20-22	12
33-34	13
30-33	14
32-40	15
32-44	16
32-47	17
43-52	18
43-56	19
48-56	20
50-57	21
52-57	22
57	23

The superomarginal plates have the upper adoral corner rounded, and may be subquadrate, usually slightly longer than high, but more often are subrhomboid, with the adoral vertical margin convex and the aboral margin concave, sometimes even rather triangular, with the adoral and dorsal margins forming a continuous rounded contour. It usually looks as if the superomarginals markedly overlap each other in adoral direction, while they actually do so only very slightly or also meet edge to edge. The superomarginals are always arranged in regular series (fig. 29*d*, *i*, *s*). The juvenile specimen with R 8-9 mm has yet only small superomarginal spines, and apparently the distal 3-4 superomarginals are still unarmed. All the other specimens bear spines on all the superomarginals, typically one spine to each plate, only very exceptionally some plates may bear 2 spines. The spine on the second superomarginal plate is usually the largest, and the other spines decrease in length gradually towards the tip of the arms. In the larger specimens all superomarginal spines look subequal at a cursory glance. The spine on the first superomarginal plate is often only small, and sometimes apparently wanting, as in a specimen with R/r 18/7 mm, but it may also be fully as long as the second spine, as e. g. in a specimen with R/r 43/13 mm, measuring here about 3 mm in length. The number of inferomarginals is the same as, or one more than that of superomarginals.

The cribriform organs number 3 in each interradius in all the specimens. They increase in width with growth so that they almost coalesce in the large specimens.

The terminal ossicle is about half as high as broad, and forms an inconspicuous termination of the arm tip. It bears typically 3 or 5 conical spines, a distal terminal one, and a pair of slightly smaller subterminal ones (fig. 29*l*), and possibly an additional pair of proximal dorsal ones, one spine to either side of the proximal notch (fig. 29*s, t*). Specimens as large as R/r 55/14 mm may have only 3 spines on each terminal ossicle; and specimens as small as R/r 20/6 mm may have terminal ossicles with 5 spines, A single specimen with R/r 48/12 mm has two pairs of subterminal spines and thus 7 terminal spines in all. In a few specimens there are 2 diverging distal terminal spines side by side, instead of the usual unpaired one, thus 6 terminal spines in all. And one specimen, R/r 50/16 mm, has, besides four normal terminal ossicles with 5 spines, one on which not only the usual distal terminal spine is replaced by 2 diverging ones, but also the proximal dorsal spine to one side reduplicated, and further the subterminal spine to the same side trebled; thus this terminal ossicle is provided with 9 spines in all.

The central and interradial areas of the disk, as far as to a line connecting the distal corners of the outermost cribriform organs, is armed with small plates with a single spinelet each, mainly rather spaced, but in a small central area forming a close pavement (some plates here are apparently without spinelets). A distinct apical appendage armed with very minute plates is always present.

In contracted specimens the superomarginals lie like a roof over the arms, and only a narrow strip of wrinkled skin separates the opposite series to the terminal ossicle. In well expanded specimens the superomarginal plates form a vertical margin to the arms, in the whole length of which there is then a subequally broad stretch of a thin dorsal integument with scattered small unarmed plates, up to 0.5 mm in diameter. Papulae were observable in some specimens, on the main area of the disk, and in about the same number as the spiniferous plates. The madreporic body is subcircular, with the striae stretching across in radial direction. Gonad papillae were seen in some specimens, close to the distal corner of the first superomarginal plates.

The adambulacral armature consists for the proximal half or more of the arms of an aboral segmental papilla and an adoral acicular spine. Exceptionally there are 2 adoral acicular spines besides the aboral papilla (fig. 29*r*). Distally the adambulacral armature is composed of 2, or exceptionally 3 acicular spines.

The armature of the oral ossicles generally consists, besides of the conical mouth-spine, of 2 lateral, as segmental papillae modified spines (fig. 29*g*). Some oral ossicles, exceptionally all in a specimen, are provided with 3 lateral segmental papillae (fig. 29*e*). On the proximal lateral corner of the oralia there may occur a usually small, but occasionally fairly large spine (or, very exceptionally, 2 spines side by side). A single oral ossicle was found with an additional spiniform oral spine distally to the segmental papillae (fig. 29*h*).

In the ventrolateral area there is a close pavement of generally naked plates. Two of the present 86 specimens, however, are noteworthy on account of being provided with a few, or several ventrolateral spinelets, and as this is very unusual, these specimens will be described in more detail below.

Description of two specimens of *Eremicaster gracilis* with ventrolateral spines. (Fig. 29*u-æ*).

One specimen (fig. 29*u-z*) has R/r 46/11 mm; 22 superomarginalia (with spines); 3 terminal spines; dorsal armature as usual; 26-27 adambulacralia, proximally with the usual armature of an adoral spine and an aboral segmental papilla. Oralia with 2 (in one case 3) lateral segmental papillae, and in a few cases also 1-2 proximal lateral spinelets. Ventrolateral plates arranged as usual, but a number of the more distal ones each with a single conical spine (or spinelet), about 10 in each interradius (fig. 29*x, y, z*). The specimen has two of its arms in regeneration, which shows that it has been subject to damage in life, and perhaps the development of ventrolateral

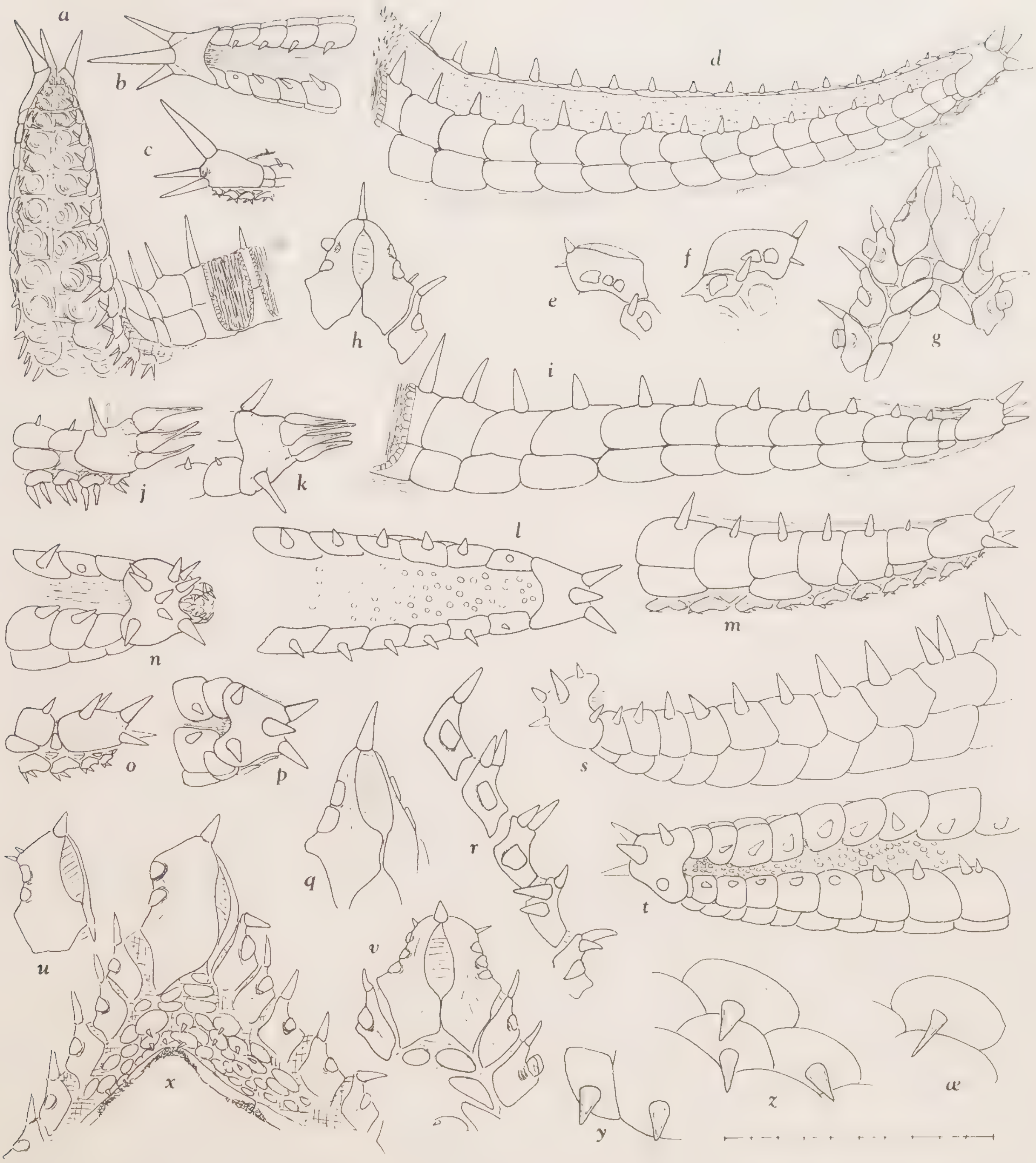

Fig. 29. *Eremicaster gracilis*. St. 716. a-c) R/r 22/6 mm, three arms in different view. d-g) R/r 32/10 mm; e-g, three jaws in different views. h-i) R/r 34/11 mm. j-k) R/r 48/12 mm, terminal ossicle in side view and in dorsal view. l-m) R/r 50/11 mm, arm in dorsal view and in side view. n) R/r 10/16 mm. o-p) R/r 52/12 mm, two terminal ossicles in side view and in dorsal view respectively. q) R/r 51/13 mm. r) R/r 52/14 mm, adambulacralia nos. 6-10. s) R/r 51/15 mm. t) R/r 55/15 mm. u-z) R/r 46/11 mm; u-v, different jaws; y-z, two groups of ventrolateral spinelets, in four times the usual scale. æ) R/r 46/15 mm, ventrolateral spinelet in four times the usual scale.
Scale: 10 mm (in y-æ: 2.5 mm).

spines is caused by irritation of the integument. The specimen is also infested with a commensalistic hydroid.

The other specimen has R/r 46/15 mm; 18 superomarginalia, with rather broad and flattened spines; 5 terminal spines; dorsal side typical; adambulacral and oral armature also typical. Ventrolateral plates in the typical arrangement, but in three of the interradii with 1 to 3-4 scattered plates each with a single slender spinelet (fig. 29 *æ*).

The ventrolateral spines or spinelets in these two specimens are very unlike each other in general appearance (cf. fig. 29*z* and 29*æ*). Ventrolateral spines probably may be easily lost in the preserved speccimens, and so perhaps also other of the specimens had ventrolateral spines in life. On the other hand, the first mentioned of the two spiniferous specimens is in a poor state, rather distorted and torn, but nevertheless still with its ventral spine-armature preserved.

These two specimens agree in the possession of a ventrolateral spine-armature with *E. pacificus*, but they are easily distinguished from this species in e. g. the shape of the terminal ossicles and the appearance of the outer series of covering papillae in the cribriform organs. The ventral spine-armature in *E. pacificus* has also a different general appearance.

Biological remarks:

Supposedly ripe eggs were found in the gonads of a couple of specimens with R/r 48/13 and 50/13 mm. They are slightly oval in shape and have a greater diameter of 0.5-0.6 mm. (Ludwig in 1905, p. 97, recorded 0.6 mm large eggs from a specimen of his *Porcellanaster waltharii (= E. gracilis)* with R 42 mm).

One specimen with R/r 47/15 mm appears to be infested with an ascothoracid, since in one radius of the disk there is a pair of close-set holes surrounded by a thickened wall of the integument.

Four specimens, the one with R/r 46/11 mm and ventrolateral spines, and three others with R/r 22/6, 47/15 and 50/15 mm respectively, are all infested with a commensalistic athecate hydroid, in a number of one to about half a dozen individuals on each sea-star, mostly attached to the ventral side, round the mouth on the peristome proximally to the series of tube-feet, or for instance on the jaws, but one hydroid is also found on the dorsal side close to the fifth superomarginal plate.

Distribution:

Eremicaster gracilis (syn. *tenebrarius)* is up to the present day collected in 18 dredgings in the eastern Pacific, off the American coast from northern Chile to southern Alaska, and is further recorded from the recent Russian explorations of the deep-sea near Kamchatka (fig. 39). It has been found at depths between 2690 and 5204 m, mainly on a bottom of mud (grey, blue, green) or globigerina ooze, but also on diatom ooze, sand and muddish clay. The temperatures recorded range from 1.3° to 2.6°C.

Eremicaster pacificus (Ludwig, 1905)

Porcellanaster pacificus n. sp., Ludwig 1905 pp. 89-92, pl. $6_{28\text{-}29}$.

Eremicaster pacificus, Fisher 1911 pp. 29-31, pl. $2_{1\text{-}3}$.

Eremicaster pacificus, H. L. Clark 1913 p. 187.

Eremicaster pacificus, H. L. Clark 1920 p. 76.

Non: *Eremicaster pacificus,* Madsen 1951 pp. 76-78, fig. 1. *(= E. vicinus).*

Nec: *Eremicaster pacificus,* Madsen 1956 pp. 26-27. *(= E. vicinus).*

This species was described by Ludwig (1905) from 21 specimens collected by the Albatross in seven dredgings in the eastern tropical Pacific in the Panamic region (st. 3360: 6°17′N, 82°05′W, 3058 m, fine black and green sand, 2.4°C.; st. 3362: 5°56′N, 85°11′W, 2149 m, green mud, sand and stones, 2.7°C.; st. 3376: 3°09′N, 82°08′W, 2070 m, globigerina ooze, 2.4°C.; st. 3392: 7°06′N, 79°40′W, 2323 m, hard Rhabdamnina bottom, 2.4°C.; st. 3400: 0°36′S, 86°46′W, 2418 m, globigerina ooze, 2.2°C.; st. 3411: 0°54′N, 91°09′W, 2174 m, globigerina ooze, 2.4°C.; and st. 3415: 14°46′N, 98°40′W, 3436 m, globigerina ooze, 2.2°C.).

Fisher in 1911 added the record and description of 6 specimens from three Albatross dredgings in the Bering Sea and in the eastern North Pacific, off southern Alaska and off Washington (st. 3603: Bering Sea, between Pribilof and Umnak Islands, 3239 m, brown ooze; st. 2859: off Prince of Wales Island, southern Alaska, 2870 m, 1.6°C.; and st. 3075: off Washington, 1571 m, green mud). H. L. Clark in 1913 recorded 11 specimens from three Albatross dredgings west of Lower California (st. 5673: off Point San Tomas, 1994 m; st. 5691: off Point San Tomas, 1588 m, 2.9°C.; and st. 5692: off Point San Tomas, 1968 m, 2.8°C.). And in 1920 H. L. Clark finally recorded 2 specimens dredged by the Albatross at two stations off Peru (st. 4647: 4°33′S, 87°43′W, 3667 m, globigerina ooze, 1.9°C.; and st. 4649: 5°17′S, 85°20′W, 4088, grey mud, 1.9°C.

(The present author formerly believed that Ludwig's *E. vicinus* of 1905 was a form of *E. pacificus*, and under this latter name recorded (Madsen 1951, 1956), from the Swedish Deep-Sea Expedition and the Galathea Expedition, some specimens which, as was also stated in the text, conformed to the description of *P. vicinus*. *Eremicaster vicinus,* however, is now recognized as a distinct species, cf. below).

LUDWIG (1905) gave the size of 10 of his 21 original specimens as follows, R/r in mm with the number of superomarginals added in parentheses: 14/7 (7), 15/7.5 (6), 16/8 (6). 17/8 (7), 19/8 (8), 22/10 (8), 23/10 (8), 24/12 (8), 26/12 (9), and 28/11 (9). The characters of his material are: Superomarginals each with an erect dorsal spine; always 3 well developed cribriform organs of a lamelliform structure. Terminal ossicles with 5 or 7 spines, viz. one or two proximal pairs besides the usual 3 distal spines. Dorsal side of disk centrally and interradially with small plates, each with a spinelet, and arm bases and arms with spaced small naked plates. A distinct apical appendage. Papulae in main disk area. Adambulacralia with diverging acicular furrow spines (in median part of arm 8 adambulacralia corresponding to 6 inferomarginalia). Oralia with 2-4, usually 3, acicular lateral marginal spines, besides the common conical mouth-spine. Ventrolateral plates each armed with a short spinelet.

One of the six specimens recorded by FISHER (1911) has R/r 21/10 mm; 8-9 superomarginals, with 1 (2) spines; terminal ossicles, besides the usual 3 spines, provided with 2-5 pairs of proximal dorsal spines (lacking, however, in a small specimen); main part of disk with spaced spinelets (occasionally also 2-3 isolated spinelets on outer part of arm); an apical appendage; adambulacralia with 2 sharp spinelets; oralia with an acicular mouth-spine, common to the combined pair of oralia, and 2-5 similar lateral spines; ventrolateral plates with spinelets similar to the dorsal ones.

H. L. CLARK (1913) records R in his 11 specimens as ranging from 8 to 24 mm. The specimen with R 8 mm had 5-6 superomarginalia, most of them with a spine, and 8-9 adambulacralia. The two specimens recorded by CLARK in 1920 had R 15 and 22 mm.

The characters which should distinguish *E. pacificus* from *E. crassus* and *E. gracilis (tenebrarius)* are firstly the presence of ventrolateral spinelets, and secondly that the furrow spines are never modified as segmental papillae. However, these characters alone would not be sufficient for distinguishing *E. pacificus* with certainty. Thus in populations of *E. gracilis* specimens may occasionally occur which have ventrolateral spines, though in the cases known conical or acicular, whereas those in *E. pacificus* are rather terete. And in populations of *E. crassus* there may be many specimens in which all the adambulacral and oral spines are spiniform, none of them being modified as segmental papillae.

Through the courtesy of dr. *Deichmann* of the Museum of Comparative Zoology, the present author has been enabled to examine one of H. L. CLARK's specimens from the Albatross st. 5691. This re-examination has shown that further differences distinguishing *E. pacificus* from *E. crassus* and *E. gracilis,* may be e. g. the shorter, broader and proximally more deeply concave terminal ossicle and possibly also a more complete dorsal pavement of plates in the arms, a character, however, which may be individually variable. The shape of the single papillae of the covering outer series in the cribriform organs affords a distinguishing character too, being very large quadrangular ones in *E. pacificus,* but not especially conspicuous in the other species.

Distribution:

Eremicaster pacificus is known from fourteen dredgings in the eastern Pacific, from the Bering Sea to Peru (fig. 40), in depths of 1571 to 4088 m, on a bottom of sand or mud or globigerina ooze, and at temperatures ranging from 1.6° to 2.9° C. It has further been taken in the western North-Pacific (the Bering Sea) by the Vitjaz.

Eremicaster vicinus (Ludwig, 1907)

Fig. 30.

Porcellanaster vicinus n. sp., LUDWIG 1907 p. 318.

Porcellanaster vicinus var. *inermis* n. sp., LUDWIG 1907 p. 318.

Eremicaster vicinus, H. L. CLARK 1920 pp. 77-78, pl. 2_{7-8}.

Eremicaster pacificus, MADSEN 1951 pp. 76-78, fig. 1. (Non *pacificus* Ludwig).

Eremicaster pacificus, MADSEN 1956 pp. 26-27. (Non *pacificus* Ludwig).

LUDWIG in 1907 gave a preliminary description of this species, and of a separate variety, based on some specimens collected by the Albatross expeditions in the eastern tropical Pacific (off Peru); and H. L. CLARK in 1920 briefly dealt with the same material and published photographs of one specimen. The type-locality of *P. vicinus* (according to H. L. CLARK) is the Albatross st. 4670 (12°08′S, 79°02′W, 5869 m, fine dark brown mud, 1.9° C.), and specimens by LUDWIG registered as *P. vicinus* var. *inermis* were taken at the same station and at the neighbouring st. 4672 (13°12′S, 78°18′W, 5204 m, fine, dark, brown mud, 1.8° C.). H. L. CLARK, who does not keep the variety distinct, records 44 specimens from the former station and 2 specimens from the latter.

The specimens described of *E. vicinus* (inclusive of the variety *inermis*, which is distinguished only by the lack of superomarginal spines) range in size from R 9.5 mm over R/r 17/8, 21/10 (the type of *vicinus)* and 24/10 mm to R 32 mm. The number of superomarginalia is 4 in the small specimens, 7 in the medium-sized ones, and 10 in the large ones. Superomarginals of arm angle, at least first two, without spines, and sometimes all superomarginals naked (var. *inermis)*, but otherwise the superomarginal plates of the arms with single spines. Three cribriform organs. Terminal ossicles with 3 spines. Dorsal side with scattered spinelets each on its own small plate. Adambulacralia with 2 spines. Oralia with 1-2 minute lateral spines besides the common mouth-spine. Ventrolateral plates naked.

LUDWIG noted that his new species *P. vicinus* was distinguished from the otherwise closely related *P. pacificus*, firstly by the complete absence of ventrolateral spines, secondly by having only 1 (or rarely 2) minute lateral oral spines, and thirdly by the absence of spines on the superomarginals of the arm angle; and LUDWIG further notes that the terminal ossicles bear ventrally only one pair of spinelets, instead of two pairs. Taken separately these differences are not very important in taxonomical respect. The absence of ventrolateral spines seems to offer the most reliable distinguishing character, but the presence or absence of ventrolateral spines is individually variable in e. g. *Porcellanaster cæruleus* and also in the above described population of *Eremicaster gracilis*. The absence of superomarginal spines in the arm angles is only a poor character, and the same applies to the low number of lateral oral spines. LUDWIG himself recorded the number of lateral oral spines in his *P. pacificus* as 2-3, rarely 4. From LUDWIG's own description of *P. pacificus* it also appears that a single pair of subterminal spines is the usual. The evidence drawn from these considerations therefore supports FISHER's conclusion, 1911 p. 30, that *vicinus* "is insecurely separated from *pacificus*".

H. L. CLARK in 1920, when dealing with LUDWIG's material, maintained *E. vicinus* as a separate species and noted that he did not think that FISHER would consider *E. vicinus* insecurely separated from *pacificus* if he had compared specimens. And then continues: "Besides the absence of actinal interradial spinelets, *vicinus* has two characteristics which easily separate it from *pacificus*. One of these is found in the adambulacral spines, which are very small (short and slender) and are placed close together at the adoral end of the plate, while the other and more conspicuous is in the spinulation of the oral plates, which have only one, or sometimes two minute conical spinelets near the center of the margin. While the abactinal surface of *vicinus* is thus indistinguishable, by any constant character, from that of *pacificus*, the oral surface is separable at a glance."

The differences stated by CLARK, however, do not at all prove the specific validity of *E. vicinus*. FISHER was a most reliable taxonomical observer, and so his statement of *E. vicinus* being insecurely separated from *E. pacificus* supported the present author in recording (1951) under the name of *E. pacificus*, 2 specimens dredged by the Swedish Deep-Sea Expedition in the tropical Atlantic (st. 329: about 9°44'N, 26°25'W, 5610-5600 m, calcareous red clay, 2.4° C.), though these specimens, as stated in the text, agreed with the description of LUDWIG's *vicinus*. In 1956 the present author further recorded under the name of *pacificus* 9 specimens from two hadal dredgings by the Galathea in the Sunda Trench and in the Kermadec Trench respectively, which too – as stated in the text – agreed with LUDWIG's description of *vicinus* var. *inermis*.

The study of the large Galathea-material of *Eremicaster*, and the re-examination of a specimen of *E. pacificus* from the Albatross collections, besides a re-examination of one of LUDWIG's original specimens of *vicinus* (from Albatross st. 4670) – also through the courtesy of Dr. DEICHMANN – have, however, induced the present author to amend his former view on *E. vicinus*.

LUDWIG's *vicinus* is undoubtedly a distinct form, and probably of specific rank, although related to *E. pacificus*. It is distinguished from *E. crassus* and *E. gracilis* by having the arms and arm bases (outwards of the outermost cribriform organ) more or less completely paved with fairly large naked plates, considerably larger than the spine-bearing ones of the disk area; by having a central area on the disk paved with plates somewhat larger than those of the main part, by lacking a distinct apical appendage, though, according to CLARK's photo fig. 7 pl. 2, possibly with an apical cone; and further by having a weaker furrow armature. What distinguishes *E. vicinus* from *E. pacificus*, is the shape of the terminal ossicle: less broad and with only 3 spines (the number of spines on the terminal ossicle, however, is a very poor character); the appearance in the cri-

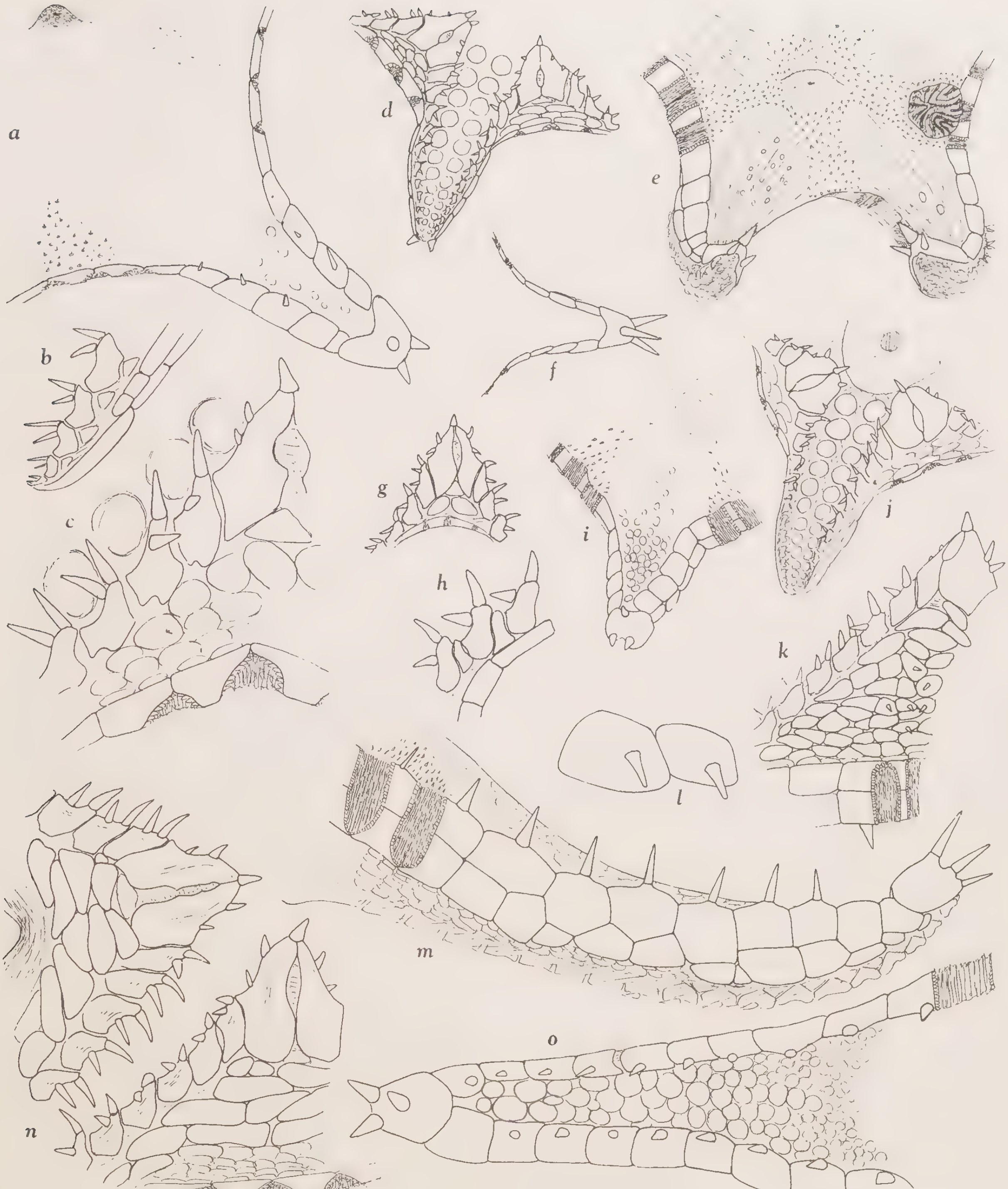

Fig. 30. *Eremicaster vicinus*. a-c) Swedish Deep-Sea Expedition st. 329; b-c, distal adambulacralia and part of ventral side, in twice the usual scale. d-j) Galathea st. 465. d) R/r 11/4.5 mm. e) R/r 14/5-6 mm. f) R/r 8-10/4 mm. g-h) R/r 12/5 mm; h, adambulacralia nos. 4-6 in twice the usual scale. i-j) R/r 11/4.5 mm. k-o) Galathea st. 650. k-m) R/r 25/8 mm; l, ventrolateral spinelets in four times the usual scale. n-o) R/r 30/9 mm; n, part of ventral side, showing two jaws.
Scale: 10 mm (in b-c, and h: 5 mm, in l: 2.5 mm).

briform organs of the papillae in the outer covering series: not especially enlarged; and the absence of a distinct apical appendage, at least in specimens of some size. Also the usually naked ventrolateral plates may distinguish *E. vicinus* from *E. pacificus*, but as will appear from the re-description of the Galathea specimens, some specimens of *E. vicinus* may show scattered ventrolateral spinelets.

The two specimens which were described from the Swedish Deep-Sea Expedition in the Atlantic, have R/r 18-19/8 (fig. 30*a-c*) and 19-20/8 mm; 6-7 and 8-9 superomarginalia; and both of them 13-14 adambulacralia. Superomarginal plates of arms with spines, but those in arm angle naked. Three terminal spines. One of the specimens in one interradius has 4 instead of the usual 3 cribriform organs. Dorsal side of disk with small plates carrying single spinelets, and with a small apical cone; spaced naked plates in the arms. Adambulacralia with 2 small furrow spines. Oralia with 2 small distally placed lateral spines, besides the common mouth-spine. Ventrolateral plates naked.

The Galathea material:

Specimens of *Eremicaster vicinus* were collected, as the only porcellanasterids, in two of the hadal dredgings undertaken during the Galathea Expedition, in the Java Trench and in the Kermadec Trench respectively.

St. 465: 10°20'S, 109°55'E, 7000-6900 m, 2.1°C. 5 specimens.

St. 650: 32°20'S, 176°54'E, 6620-6730 m, 1.3°C., brown clay with pumice. 3 (or 4) specimens.

(The depths recorded in 1956 had to be slightly revised).

The specimens from st. 465 in the Java Trench are juveniles, ranging in size from R/r ab. 8-10/4 to 14/5-6 mm.

R/r in mm	Number of superomarginalia	Number of adambulacralia
about 9/4	5	9(-10)
11/4.5	5-6	10-11
11/4.5	6	12
12/5	6	9-10
14/5-6	6	12

The two first-mentioned specimens show the juvenile character of a close pavement of unarmed perforated plates dorsally, these embryonic plates being the only dorsal skeleton. In the third specimen mentioned, scattered spinelets occur interradially (fig. 30*i*), and in the two last-mentioned and slightly larger specimens there are distinct interradial bands of spinelets. The largest specimen is provided with a distinct apical cone (fig. 30*e*). (And it certainly appears as if there is a central pore in this cone?). The superomarginals are subquadrate and are all unarmed (fig. 30*e, i*). Three cribriform organs. Terminal ossicles with 3 spines. Adambulacralia with 2 spines (fig. 30*d, g, h, j*). Oralia with 1-2 (3) small lateral spines, besides the common mouth-spine (fig. 30*d, g, i*). Ventrolateral plates naked (fig. 30*d, g*).

The three specimens from st. 650 in the Kermadec Trench are fairly large ones (a fourth much damaged specimen of sub-equal size was found in the meshes of the trawl after the attempted dredging at st. 656 but, since in all probability bottom was not reached, must have been overlooked when the trawl was emptied after the haul at st. 650).

R/r in mm	Number of superomarginalia	Number of adambulacralia
25/8	9/10	18
29/10	11	29
30/9	11	20

The superomarginals are subquadrate or slightly longer than high, and the inferomarginals of the arms are not much lower than their superomarginal companions. The superomarginals each bears a single slender dorsal spine, except sometimes the last ones, and possibly also the first one. The spine on the first superomarginal plate at least is always smaller than the others (fig. 30*m*). The 3 cribriform organs all show the characteristic subquadrate covering papillae. The terminal ossicles bear 3 spines in two specimens (fig. 30*o*), but 5 in the third, here being two pairs of subterminal ones (fig. 30*m*). The median and interradial area of the disk is armed with close-set small rounded plates each with a spinelet, and there are scattered papulae. There is an apical cone, but nothing like a distinct apical appendage as in the other forms of *Eremicaster*. In the arms and the arm-bases, delimited from the disk by a line connecting the distal corners of the outer cribriform organs, there is a close pavement of plates (fig. 30*o*), somewhat larger than the spiniferous ones. The adambulacralia bear 2 spines. The oralia have 2 lateral spines besides the mouth-spine (fig. 30*n*). The ventrolateral plates are usually naked, but the re-examination now undertaken revealed that one of the specimens has single conical spinelets on a small number of the median ventrolateral plates in one interradius (fig. 30*k, l*).

The occurrence of ventrolateral spines in one of these specimens confirms that the possession of these is of doubtful taxonomic value, and reduces the difference between *E. vicinus* and *E. pacificus*. But, as mentioned above, e. g. the different shape of the terminal ossicles, the different development of the apical prominence, and the different appearance of the outer papillae in the cribriform organs separate the two forms.

The presence of a close pavement of fairly large plates in the arms of the Galathea specimens is a character which they share with the original specimens of *vicinus*, as has been ascertained by a reexamination of one of these, and as can be seen on the photograph published by H. L. CLARK (1920). Such a close armature is not found, however, in the Atlantic specimens from the Swedish Deep-Sea Expedition. Apparently the dorsal armature of plates in the arms of *E. pacificus* may be subject to a similar individual variation, and thus the feature can hardly be used in separating an Atlantic form of *vicinus* from a Pacific form.

Distribution:

Eremicaster vicinus has been found in a small number of dredgings in the deeper parts of the three great oceans (fig. 40), one in the mid-Atlantic, one in the Indian Ocean in the Java Trench, and a few in the Pacific, one of which in the Kermadec Trench, and the two others off Peru. Further it has recently been dredged in the North Pacific by the Vitjaz. The form is recorded taken at depths from 5204 to 7245 m, on mud and calcareous clay, and at temperatures between 1.3° and 2.4°C.

Apparently *Eremicaster vicinus* is the hadal representative of *Eremicaster pacificus*.

Sidonaster Koehler, 1909

Type-species: *Sidonaster vaneyi* Koehler, 1909.

Diagnosis:

Porcellanasterids with opposite superomarginals separate in whole arm length, and each with a dorsal spinelet. A mid-interradial suture. A single cribriform organ of a papilliform structure. A single proximal, enlarged mouth-spine, common to both oralia forming a jaw. Terminal ossicle distal to arm end, subcrescentic, much broader than long.

Description:

The general appearance of this genus is the same as that of *Porcellanaster* s. str., except for the shorter terminal ossicle and for the larger and papilliform cribriform organ. It may further be distinguished from *Porcellanaster* by the relatively larger (and hence in relation to length of R fewer) adambulacralia (and podia).

The single papilliform cribriform organ is very large, and with the calcareous papillae longer and more slender than in any other porcellanasterid. The rows of covering papillae extend from one outer dorsal corner continuously around the organ along the lateral and ventral side to the other dorsal corner. The first superomarginal plate, with the cribriform organ, is very much larger, higher and longer than the following ones, which are subquadrate, but with the adoral dorsal corner rounded. The superomarginals overlap with their curved adoral end more or less distinctly the aboral end of the preceding plate. All the superomarginals are armed with an erect dorsal spine of a length of up to about $1^1/_2$ times the height of the plate, and possibly with one or two accessory spinelets. The inferomarginals are less than half as high as their superomarginal companions. The terminal ossicle is deeply concave adorally and very broad in relation to its length (subcrescent-shaped), it carries 5-7 subequal spines, a distal terminal one, a pair of subterminal ones, and proximally on the dorsal surface 1-2 additional spines to either side. The disk is interradially armed with spinelets, each on its own small plate, and spinelets may occur over the whole main disk area to a line connecting the distal corners of the first superomarginals. (LIEBERKIND in 1932 p. 293 mentioned as a further character, distinguishing *Sidonaster* from *Porcellanaster* and *Eremicaster*, the occurrence in the dorsal integument of scattered calcareous rods besides the usual perforated plates, claiming it for certain that these rods really were found there and had not been derived from the stomach wall. – Minute calcareous rods is the usual skeleton in the internal tissues of the porcellanasterids). Numerous papulae is found in the main disk area. There is a distinct apical appendage. The madreporite is roundish or oval, close to the marginals, and with the striae radiating from a point located near its center, or between the center and the adcentral edge. The adambulacralia are rather elongate with a concave furrow margin, and a protruding adoral part on which is borne 2 diverging pointed spines (occasionally only one, or as many as 3 furrow spines). The furrow is broad and the podia are fairly large. The oral ossicles are large and broad, and, besides the single mouth-spine at their proximal junction, provided with 2-5 about as long, but more slender spines on their lateral margin. The ventrolateral area is armed with a pavement of plates, some of which with a single spinelet, extending as far as to the third inferomarginals, from where the series of inferomarginalia and adambulacralia are contiguous, but possibly with the ends of the ambulacralia showing between them. The type-specimen of *S. vaneyi*, with R/r 20/10 mm, has 5 superomarginals and 11 adambulacralia. The largest specimen of *Sidonaster* on record, R/r 36/15 mm, has 7 superomarginals and 15 adambulacralia.

Remarks:

Three nominal species of *Sidonaster* have been described: 1) the type-species *vaneyi* by KOEHLER in 1909, 2) *batheri*, also by KOEHLER in 1909, and 3) *psilonotus* by FISHER in 1913. As is discussed in the following, these however, may all be considered specifically identical.

Sidonaster vaneyi Koehler, 1909

Sidonaster vaneyi n. sp., KOEHLER 1909*a* pp. 37-39, pls. 3_6, 6_5, 10_3.
Sidonaster batheri n. sp., KOEHLER 1909*a* pp. 40-47, pls. 1_4, 2_5, 4_8.
Sidonaster psilonotus n. sp., FISHER 1913 p. 600.
Sidonaster vaneyi, FISHER 1919 pp. 35-37, pl. 3_3.
Sidonaster psilonotus, FISHER 1919 pp. 37-39, pls. $1_{2\text{-}3}$, 7_2.
Sidonaster psilonotus, DÖDERLEIN 1921 pp. 16-17, pl. $3_{2\text{-}2d}$.
Sidonaster psilonotus, LIEBERKIND 1932 pp. 291-293, text-figs. 12-13, pls. $4_{10\text{-}11}$, $7_{1\text{-}2}$.
Porcellanaster, resembling *cœruleus*, WOOD-MASON & ALCOCK 1891*a* p. 13.
Porcellanaster cœruleus, WOOD-MASON & ALCOCK 1891*b* p. 433 (Non *P. cœruleus* Wyville-Thomsen).

KOEHLER described his species *vaneyi* on the basis of a single specimen dredged by the Investigator in the Arabian Sea (st. 290: 24°53′N, 57°43′E, 1524-1340 m, green sand, 6.4°C.). It has R/r 20/10 mm; 5 superomarginals; 11 adambulacralia; terminal ossicle with 7 spines; dorsal disk area with a fairly dense armature of spinelets; oralia with 2 lateral spines besides the mouth-spine.

S. batheri, the other species which KOEHLER described in 1909, was based on 11 specimens collected by the Investigator in seven dredgings in the Arabian Sea and in the Bay of Bengal (st. 192: 15°11′N, 72°29′E, 1668-1703 m, grey ooze, 4.2°-4.6°C.; st. 194: 13°47′N, 72°04′E, 1630 m, grey ooze, 5°C.; st. 254: 11°17′N, 92°58′E, 1224 m, green mud, 6.1°C.; st. 299: 23°43′N, 58°52′E, 2376 m, green mud, 2.2°C.; st. 300: 24°16′N, 60°26′E, 2515-2130 m, green mud, 1.8°C.; st. 318: 7°28′N, 79°20′E, 1984 m, green mud, 2.7°C.; and a dredging without st. no.: 14°22′N, 74°21′E, 2070 m). The specimens range in size from R/r 13/6 to 26/10 mm, and the number of superomarginals varies from 5 to 7, independently of the size of the specimens. The species *batheri* should differ from *vaneyi* in having the dorsal spinelets restricted to narrow interradial bands besides to the central area, and in having as many as 4-5 lateral oral spines. These differences, as it will appear from the descriptions of the variation found in various populations of other porcellanasterids, are of no taxonomical importance whatsoever, and *batheri* may therefore be considered a synonym of *vaneyi*.

FISHER (1919) recorded under the name of *S. batheri* four specimens of *Sidonaster* from two Albatross dredgings in the Philippine region (st. 5215: 12°32′N, 123°35′E, 1147 m, green mud, 10.3°C.; and st. 5491: 9°24′N, 125°12′E, 1346 m, green mud, 11.3°C.). The largest specimen has R/r 36/15 mm, 5-7 superomarginals; 15 adambulacralia. Spinelets dorsally extending over an area intermediate between the spinelet-bearing areas in *vaneyi* and in KOEHLER's *batheri*; 2-4 lateral oral spines. The features of these specimens thus stresses the vagueness of the characters which KOEHLER thought distinguishing *batheri* from *vaneyi*. FISHER also notes concerning his specimens that: "It has in fact been difficult to decide what to name them."

S. psilonotus, the third and last species of *Sidonaster* described, was erected by FISHER (1913, 1919) for a single specimen dredged by the Albatross in an undefined locality in the Philippine region. It has R/r 22/11 mm; 7 superomarginal plates. Dorsal side almost completely naked, only provided with a small number of spinelets interradially near the cribriform organs (which feature should distinguish *psilonotus* specifically from *vaneyi* and *batheri)*. Terminal ossicles with only 5 spines (instead of 7 as in the other forms). Oralia with 4 lateral spines. The difference believed to distinguish *psilonotus* as a separate species, is taxonomically worthless, and *psilonotus* is thus to be regarded as a further synonym of *vaneyi*.

DÖDERLEIN (1921) under the name of *psilonotus* recorded 10 specimens of *Sidonaster*, collected by the Siboga in three dredgings in the region of the Malay Archipelago (st. 88: 0°35′N, 119°08′E, 1301 m, grey mud; st. 175: 2°38′S, 130°33′E, 1914 m, grey and green mud; and st. 211: 5°41′S, 120°46′E, 1158 m, grey mud). Two specimens had R/r 7/3 and 19/8.5 mm, and 9 superomarginals respectively, and the larger one 11 adambulacralia. All specimens had 5 terminal spines. (Döderlein notes p. 17 that the inner longitudinal row of ventrolateral plates only is well developed as far as to the third marginal plate, and from there to the end of the arm appears as a row of small triangular plates. – The latter statement, however, rests on a misinterpretation of the visible ends of the adambulacralia).

Lieberkind (1932) under the name of *psilonotus* recorded a single specimen of *Sidonaster,* dredged by the Valdivia in the western Indian Ocean off Somaliland (st. 257: 1°48′N, 45°42′E, 1644 m, globigerina ooze, blue mud, 4.6°C.). It has R/r 14/7 mm; 6-7 superomarginals; 10 adambulacralia. (Lieberkind did not give information of size or number of ossicles, but the present author has had occasion to re-examine the specimen). There are 5 terminal spines, and 4-5 lateral oral spines. Lieberkind notes that the differences between *psilonotus* and *batheri* are so unimportant that the two forms might well be only individual variations of the same species.

Wood-Mason & Alcock (1891 p. 13) mention from off Goa (Investigator st. 105: 15°02′N, 72°34′E, 1353 m, globigerina ooze, 6.7°C.) a small porcellanasterid resembling *cæruleus,* which specimen Koehler (1909*a* p. 34) after a re-examination, stated to be a *Sidonaster.* It may be added that also the specimen which Wood-Mason & Alcock (1891*b* p. 433) record from the Andaman Sea (Investigator st. 113: 12°59′N, 93°23′E, 1249 m, blue mud, 6°C.) under the name of *Porcellanaster cæruleus,* no doubt has been a *Sidonaster* too, considering the fairly high temperature at which it was found.

Distribution:

Sidonaster vaneyi, the only species in its genus, is hitherto collected in 17 dredgings (fig. 42) distributed in the northern Indian Ocean, from off the East African coast to the Malay Archipelago, the Philippines and New Guinea. It has been found at depths between 1147 and 2515-2130 m, on a bottom of grey ooze, globigerina ooze, and green and blue mud, and at temperatures ranging from 1.8° to 11.3°C.

ZOOGEOGRAPHICAL SURVEY

The Porcellanasteridae is, with a known bathymetrical range of from about one thousand to about seven thousand meters, one of the few exclusively deep-sea groups of higher taxonomic categories.

Three genera (all monotypic), *Lysaster, Benthogenia,* and *Sidonaster,* are confined – as far as is known – to the bathyal zone (depths of less than about 2000 m), and further seem to be restricted in their geographical distribution to the region of the Indian Ocean and the Malay Archipelago. (The two first mentioned are, however, recorded from only one and two finds respectively).

All other porcellanasterid genera occur in abyssal depths (i. e. are recorded from at least 2500 m), and, except *Abyssaster,* are known from all three oceans. *Hyphalaster, Thoracaster, Styracaster,* and *Abyssaster,* are exclusively abyssal. *Porcellanaster* and *Eremicaster* are also represented in bathyal depths *(P. cæruleus,* 1158-6035 m, and *E. pacificus,* 1571-4088 m). And *Eremicaster* reaches just into hadal depths *(E. vicinus,* 5204-about 7200 m).

Also a number of the species are recorded from all three oceans, and probably may be considered cosmopolitan (though perhaps in the Pacific known only from the western part, these marked with an asterisk), viz. *Hyphalaster inermis** (32 finds), *Thoracaster cylindratus* (20 finds), *Styracaster horridus** (15 finds), *Styracaster chuni** (6 finds, but yet none in the Indian Ocean), *Porcellanaster cæruleus* (86 finds), and *Eremicaster vicinus* (7 finds).

A single form, *Eremicaster pacificus* (15 finds), seems to be restricted to the eastern Pacific and the Bering Sea. Another, *Eremicaster gracilis* (23 finds), is known from the East Pacific and the western North Pacific, and has a very close relative, *E. crassus,* in the mid-Pacific and the Indian Ocean.

One species, *Styracaster elongatus* (7 finds), is recorded from both the Atlantic and the Indian Ocean. And also the species *Styracaster spinosus* occurs besides in the Atlantic (5 finds) probably also in the Indian Ocean, since the *S. clavipes* described from this region (1 find) may be the same species.

Two species, *Abyssaster tara* (8 finds) and *Styracaster armatus* (4 finds), are known from both the Indian Ocean and the western Pacific, and a third, *Eremicaster crassus* (5 finds), is known from the Indian Ocean and the mid-Pacific, and has further a very close relative, *E. gracilis,* in the East Pacific and western North Pacific.

Three species, *Hyphalaster scotiae, Styracaster ro-*

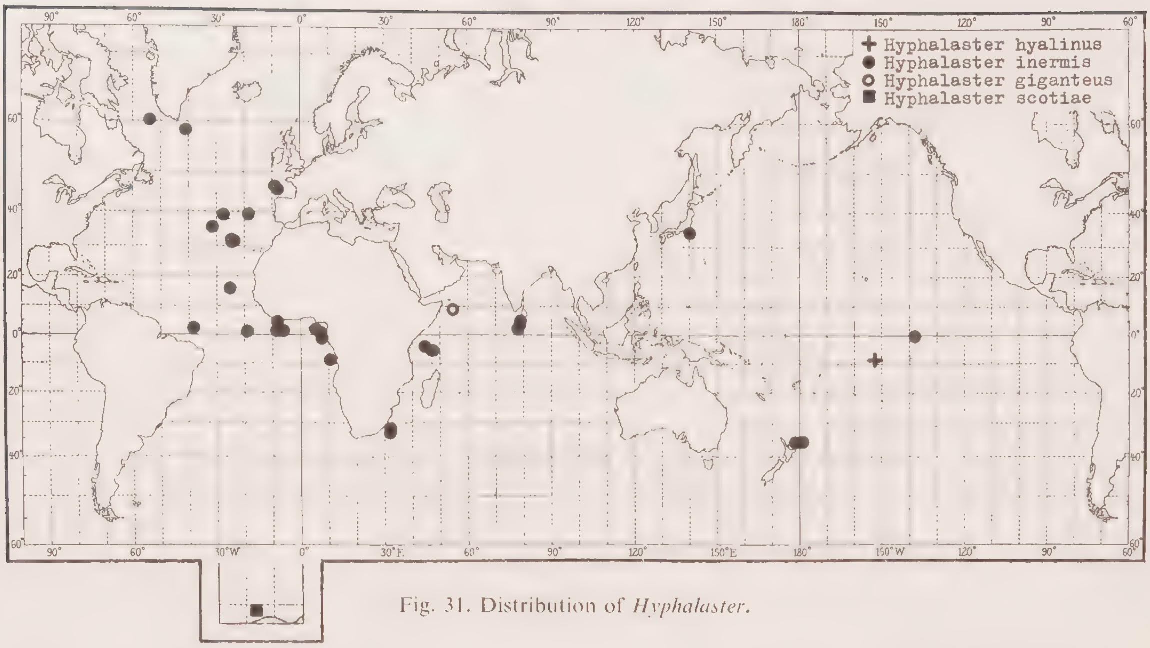
+ Hyphalaster hyalinus
● Hyphalaster inermis
○ Hyphalaster giganteus
■ Hyphalaster scotiae
30°W
0°
30°E
150°E
180°
150°W

Fig. 31. Distribution of *Hyphalaster.*

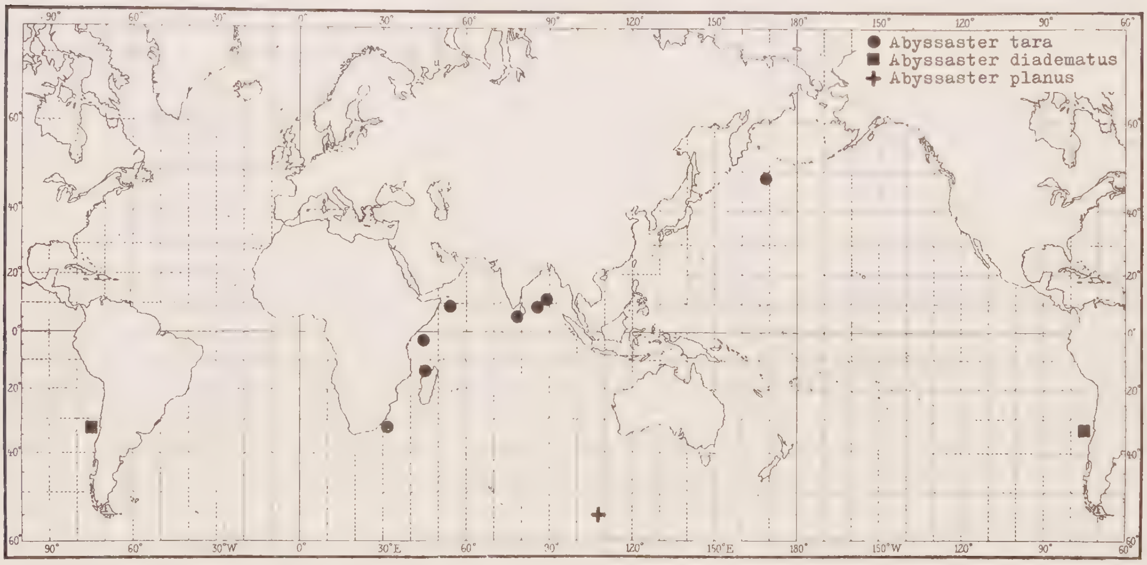
● Abyssaster tara
■ Abyssaster diadematus
+ Abyssaster planus
30°W
0°
30°E
150°E
180°
150°W

Fig. 32. Distribution of *Abyssaster.*

bustus, and *Abyssaster planus,* may be confined to the Antarctic region, but are hitherto only known from single finds.

The two porcellanasterid genera, *Porcellanaster* and *Eremicaster,* show an interesting distribution when considered together. They are the only ones known from bathyal as well as from abyssal finds, and both, as noted, may be said to have a cosmopolitan distribution. *Porcellanaster* (probably monotypic) is primarily Atlantic and Indo-West-Pacific in its distribution however (only three out of 86 records being from the eastern Pacific), while *Eremicaster* has primarily an Indo-pan-Pacific distribution (only the abysso-hadal *E. vicinus* being recorded once from the Atlantic). This pattern of distribution may perhaps indicate that *Porcellanaster* and *Eremicaster* are conquering the abyssal deep-sea from the bathyal North Atlantic and from the bathyal eastern Pacific respectively.

The main center of distribution of the Porcellanasteridae apparently is otherwise the Indo-Malayan region.

The porcellanasterids are found on a soft level bottom: greyish, greenish or bluish mud in about half of the 110 cases from which information is available; ooze in about one-third of the cases (usu-

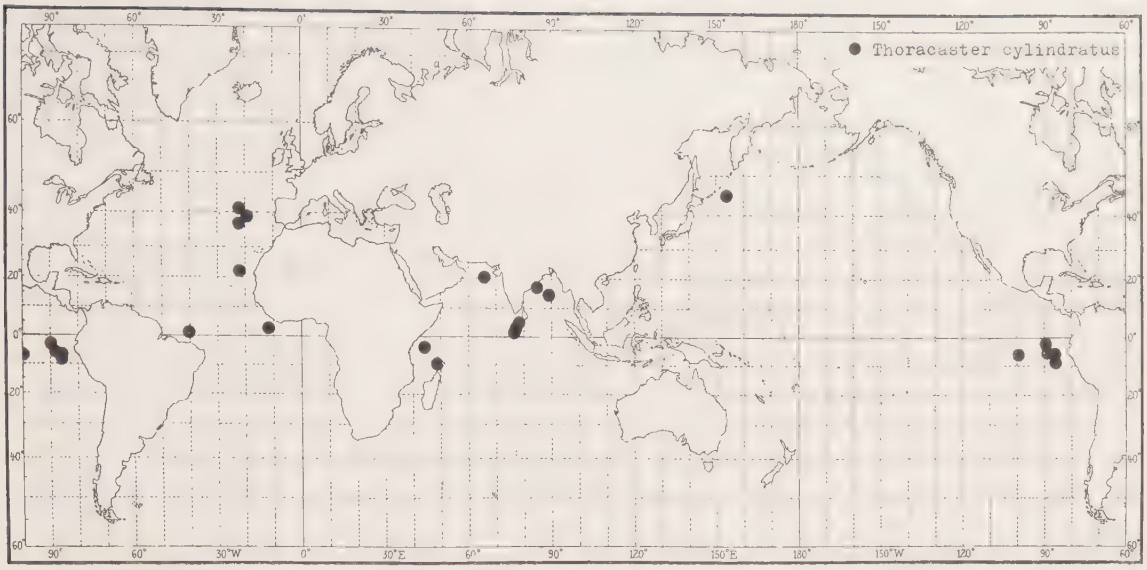
● Thoracaster cylindratus
90° 60° 30° 0° 30° 60° 90° 120° 150° 180° 150° 120° 90° 60°
60° 40° 20° 0° 20° 40° 60°
90° 60° 30°W 0° 30°E 60° 90° 120° 150°E 180° 150°W 120° 90° 60°

Fig. 33. Distribution of *Thoracaster cylindratus.*

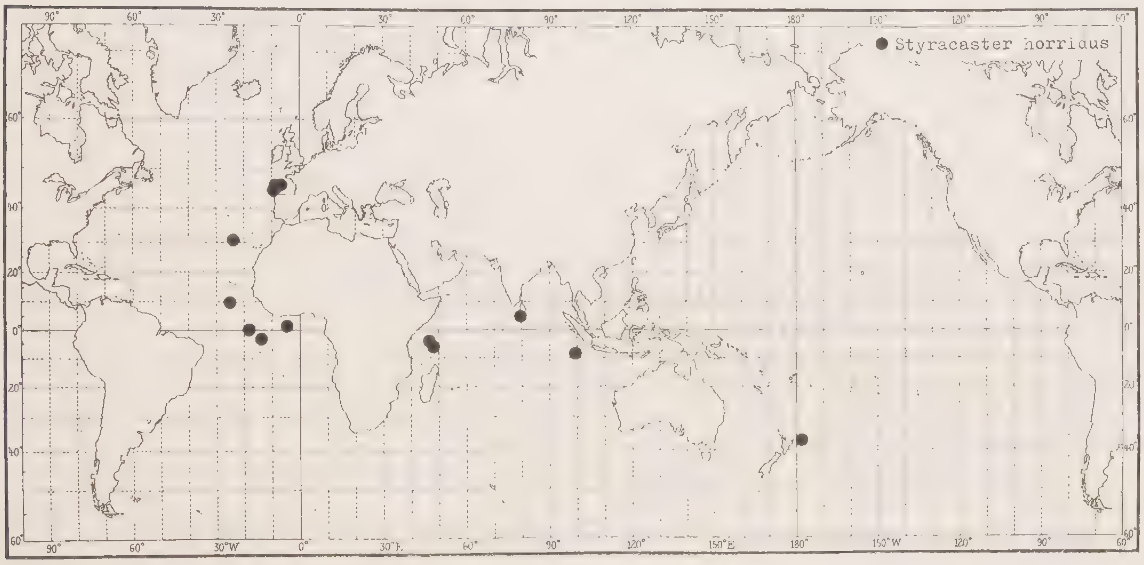
● Styracaster horridus
90° 60° 30° 0° 30° 60° 90° 120° 150° 180° 150° 120° 90° 60°
60° 40° 20° 0° 20° 40° 60°
90° 60° 30°W 0° 30°E 60° 90° 120° 150°E 180° 150°W 120° 90° 60°

Fig. 34. Distribution of *Styracaster horridus.*

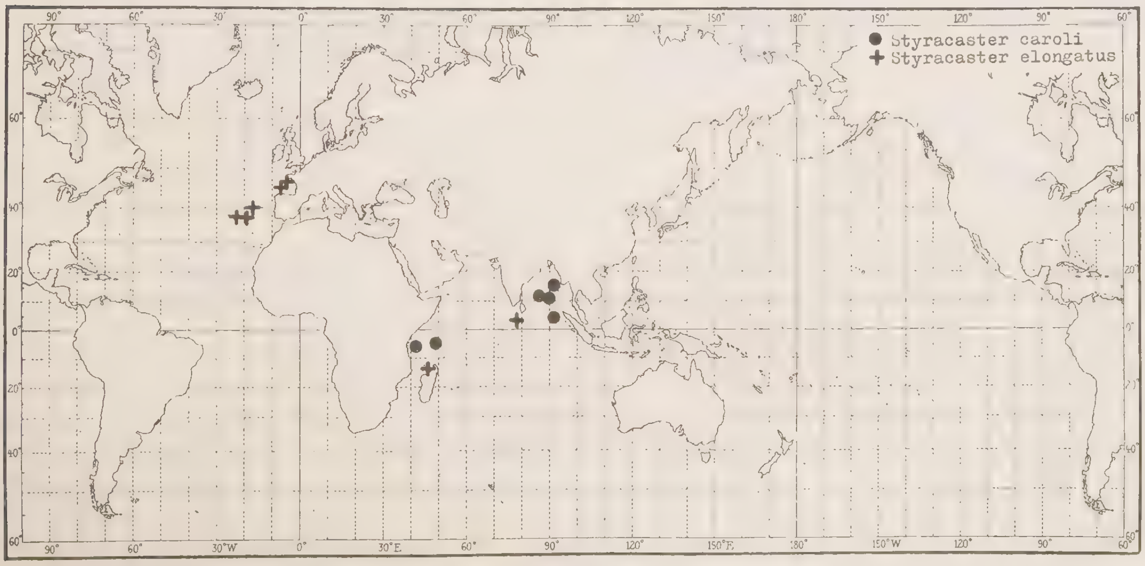
● Styracaster caroli
+ Styracaster elongatus
90° 60° 30° 0° 30° 60° 90° 120° 150° 180° 150° 120° 90° 60°
60° 40° 20° 0° 20° 40° 60°
90° 60° 30°W 0° 30°E 60° 90° 120° 150°E 180° 150°W 120° 90° 60°

Fig. 35. Distribution of *Styracaster caroli* and *S. elongatus.*

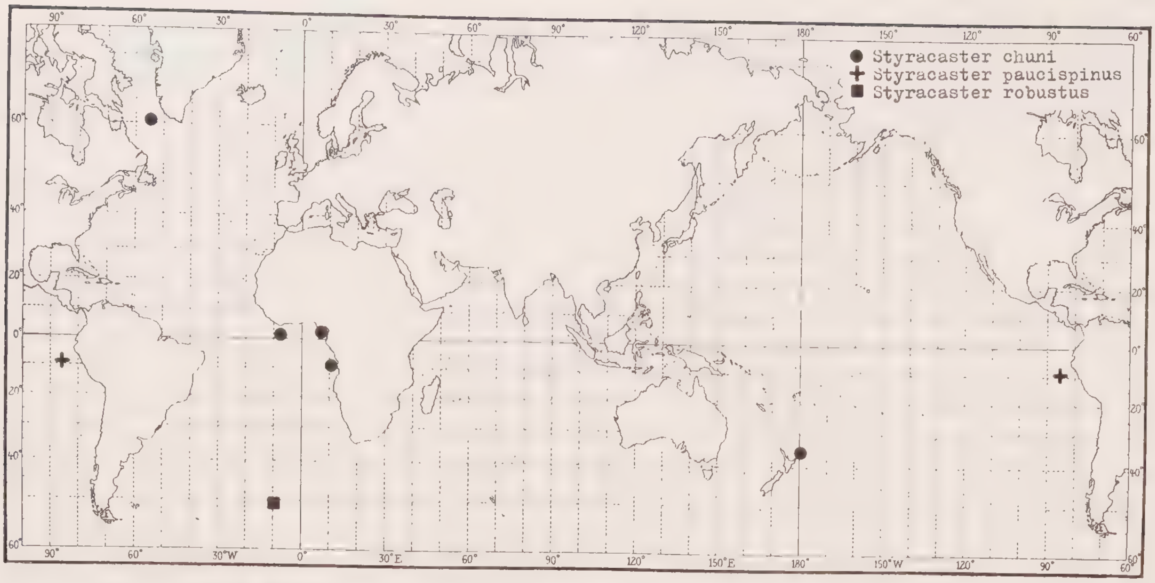
● Styracaster chuni
+ Styracaster paucispinus
■ Styracaster robustus

Fig. 36. Distribution of *Styracaster chuni*, *S. paucispinus*, and *S. robustus*.

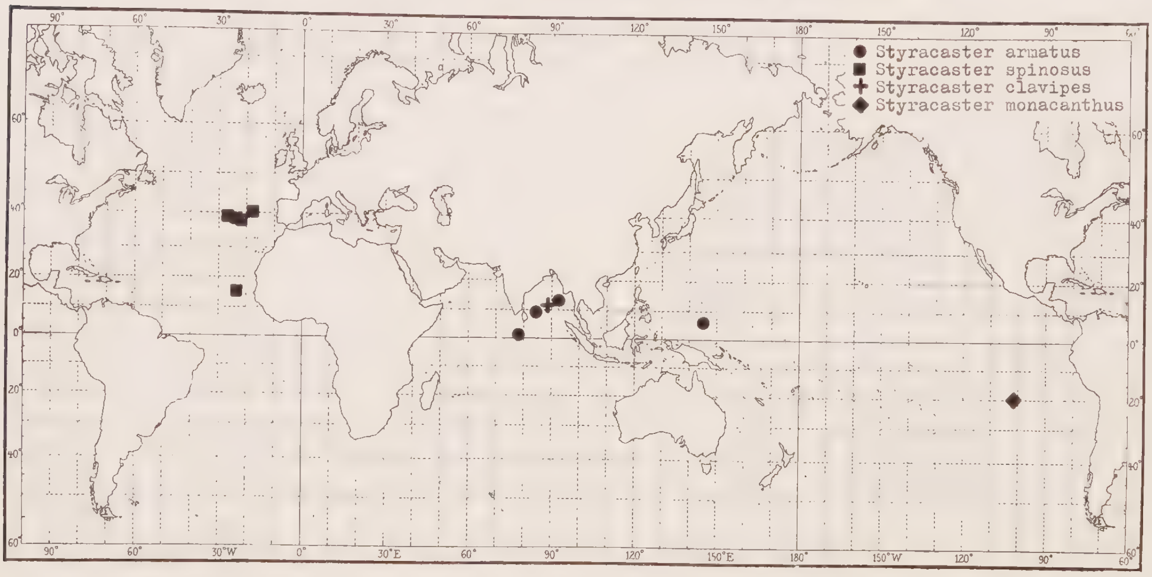
● Styracaster armatus
■ Styracaster spinosus
+ Styracaster clavipes
◆ Styracaster monacanthus

Fig. 37. Distribution of *Styracaster armatus*, *S. spinosus*, *S. clavipes*, and *S. monacanthus*.

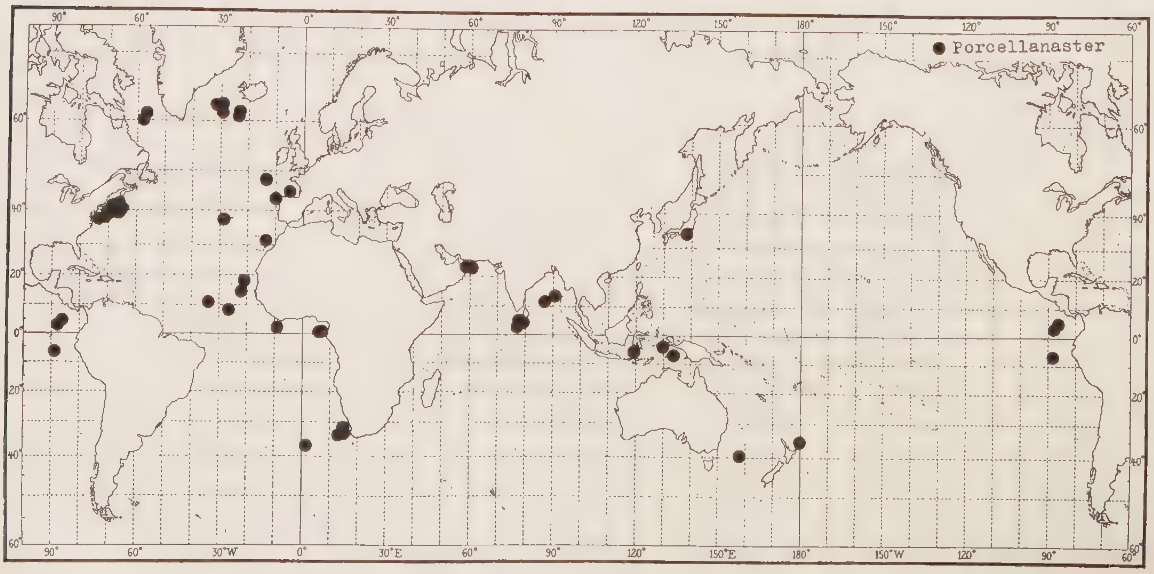
● Porcellanaster

Fig. 38. Distribution of *Porcellanaster cæruleus*.

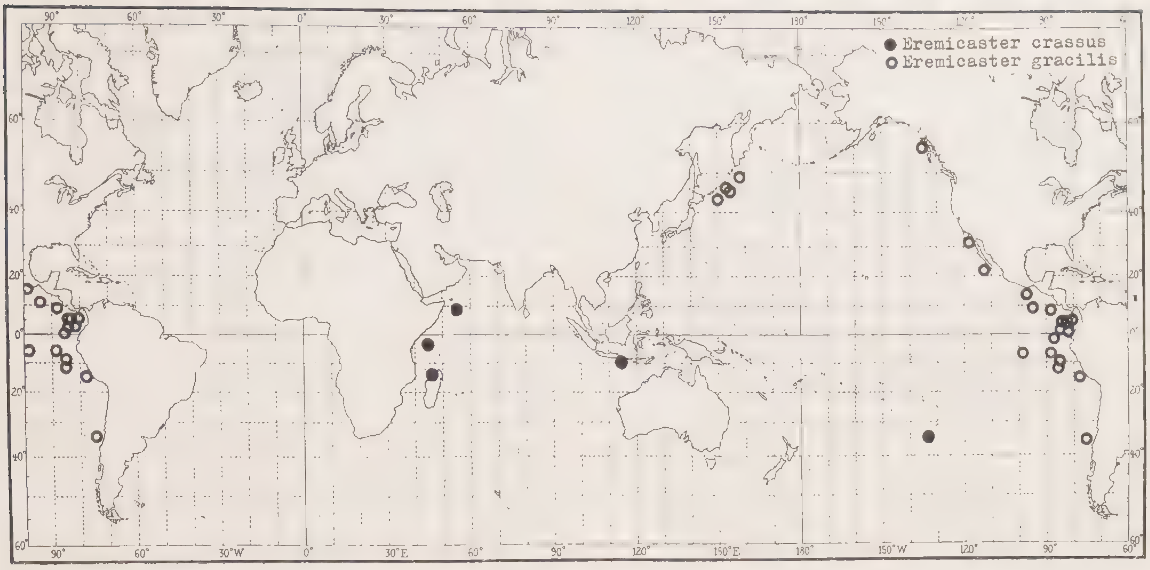
● Eremicaster crassus
○ Eremicaster gracilis

Fig. 39. Distribution of *Eremicaster crassus* and *E. gracilis*.

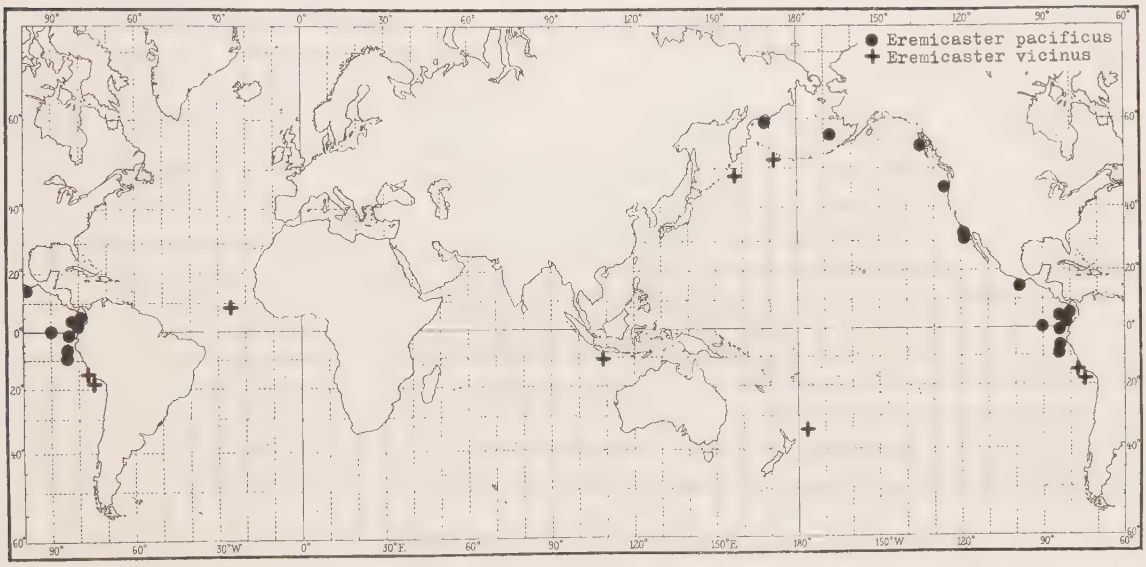
● Eremicaster pacificus
+ Eremicaster vicinus

Fig. 40. Distribution of *Eremicaster pacificus* and *E. vicinus*.

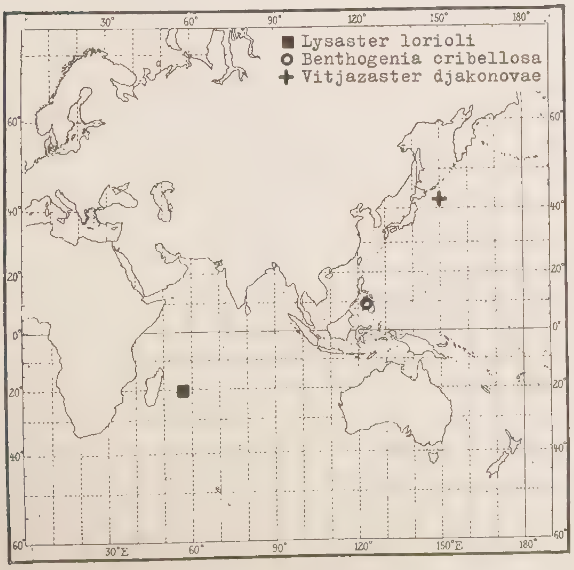
■ Lysaster lorioli
○ Benthogenia cribellosa
+ Vitjazaster djakonovae

Fig. 41. Distribution of *Lysaster*, *Benthogenia*, and *Vitjazaster*.

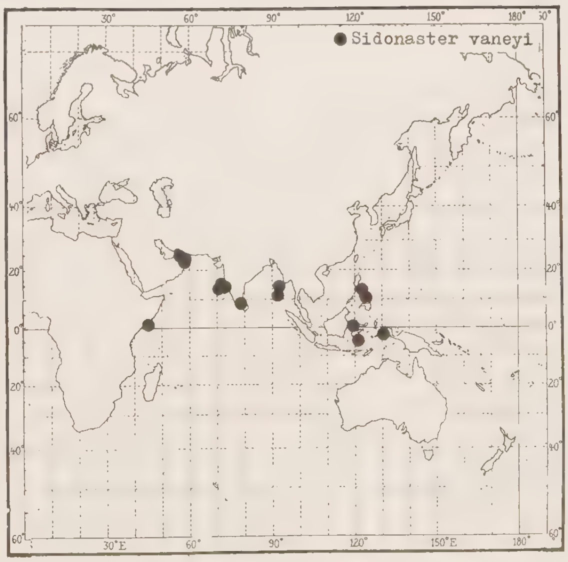
● Sidonaster vaneyi

Fig. 42. Distribution of *Sidonaster vaneyi*.

ally globigerina ooze, but in a few cases radiolarian ooze, and in one case diatom ooze); bluish, yellowish, brownish, reddish, greenish, or blackish clay in one-fifth of the cases; and, finally, green or black sand in a few cases.

The temperatures recorded for finds of porcellanasterids range from 0°C. to 11.5°C. The abyssal genera are found exclusively at temperatures below about 4°C.* Only the bathyal *Sidonaster* is thus known from the Sulu Sea in which the bottom temperature is about 10°C., and no porcellanasterids are known from the Mediterranean in which the bottom temperatures are above 12°C. Nor are any porcellanasterids known from the Arctic Sea or the Norwegian Sea with temperatures below 0°. The distribution of the porcellanasterids may to a great extent be controlled by the temperature, but it is noteworthy that no porcellanasterid has hitherto been found in shallower depths in the polar seas to where some other deep-sea groups of echinoderms have expanded their range.

Some species have a wide bathymetrical range, as *Porcellanaster cæruleus* (1158-6035 m) and *Eremicaster pacificus* (1571-4088 m), but other species known from a number of widely scattered finds were always obtained within definite zones of depths, e. g. *Styracaster horridus* (15 finds in all oceans, and all between 4040 and 5610 m) and *Eremicaster vicinus* (7 finds in all oceans, and all between 5204 and 7200 m).

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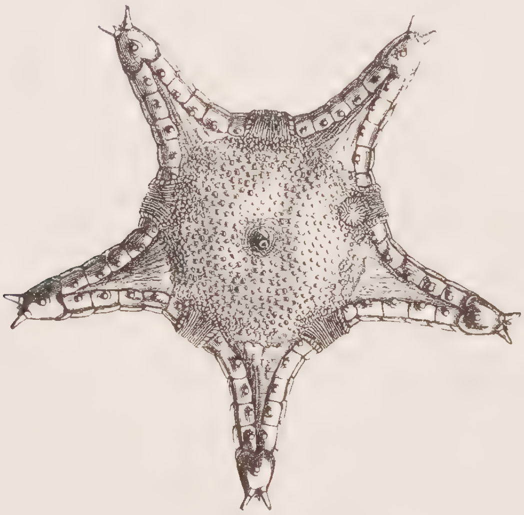
* The bottom temperatures of the Challenger stations recorded by Sladen in 1882 in centigrades were not correctly computed. The correct temperatures are given in degrees of Fahrenheit in 1889).



Porcellanaster cæruleus
The type-specimen, from Wyville Thomson, 1877 fig. 98.
Nat. size.

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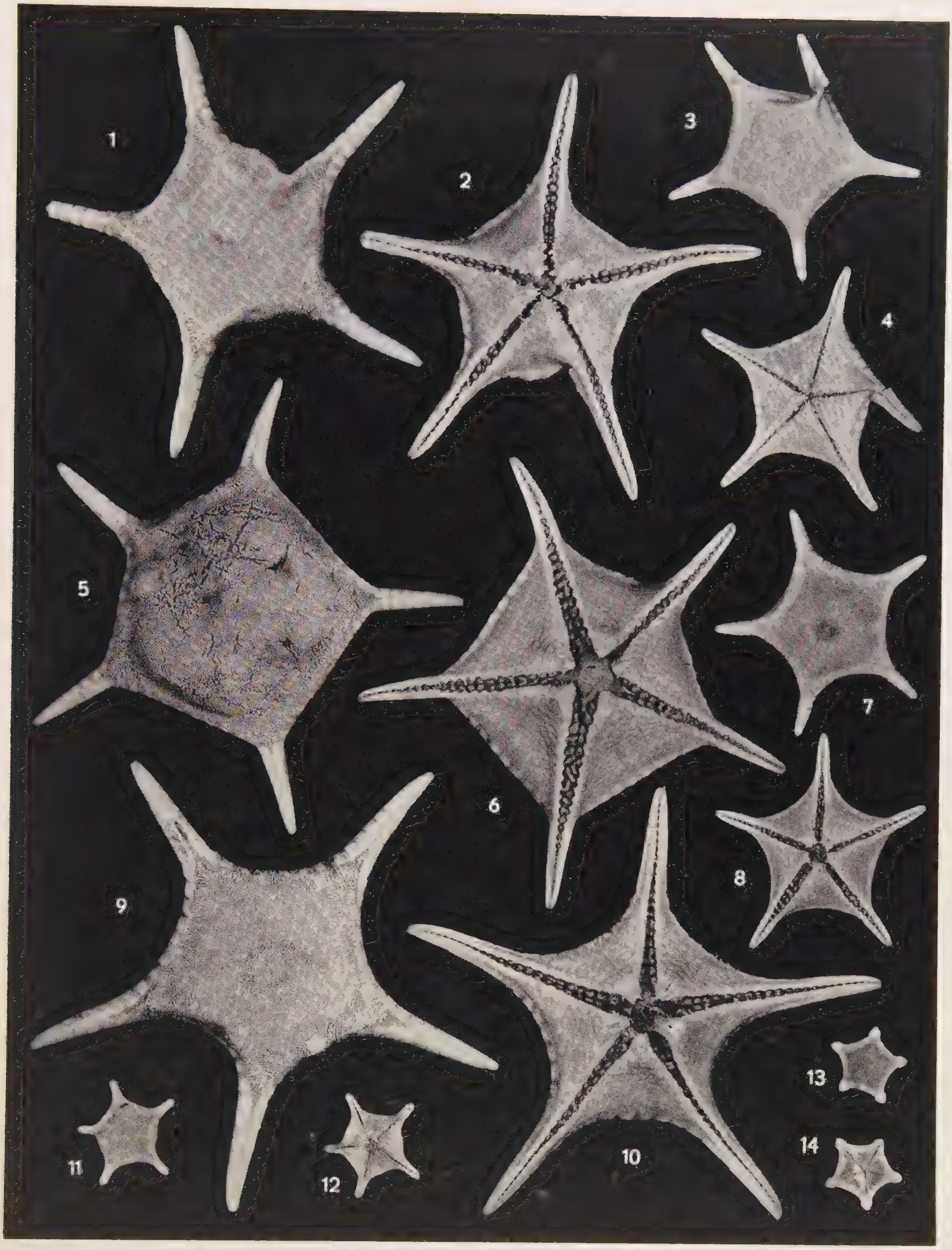
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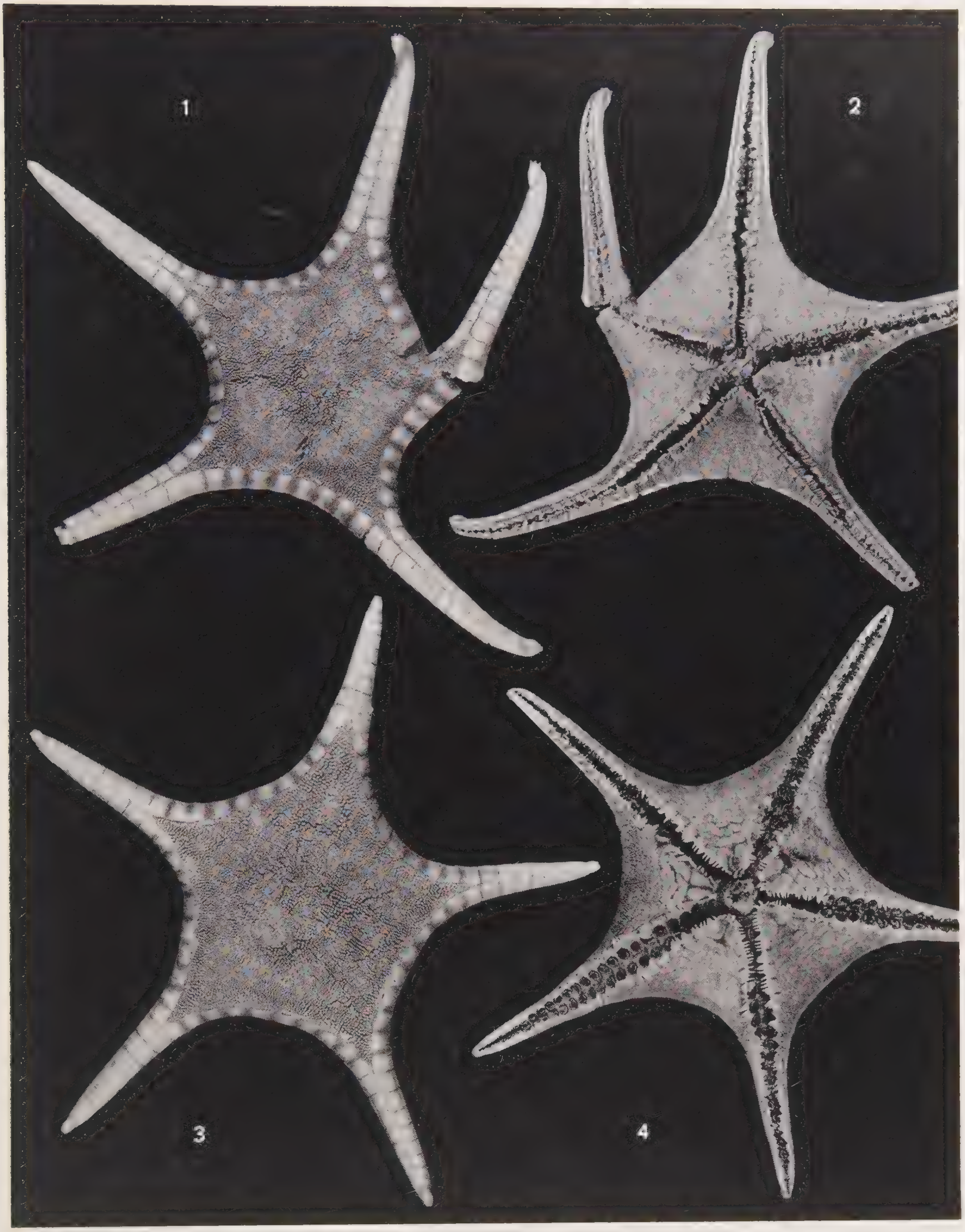

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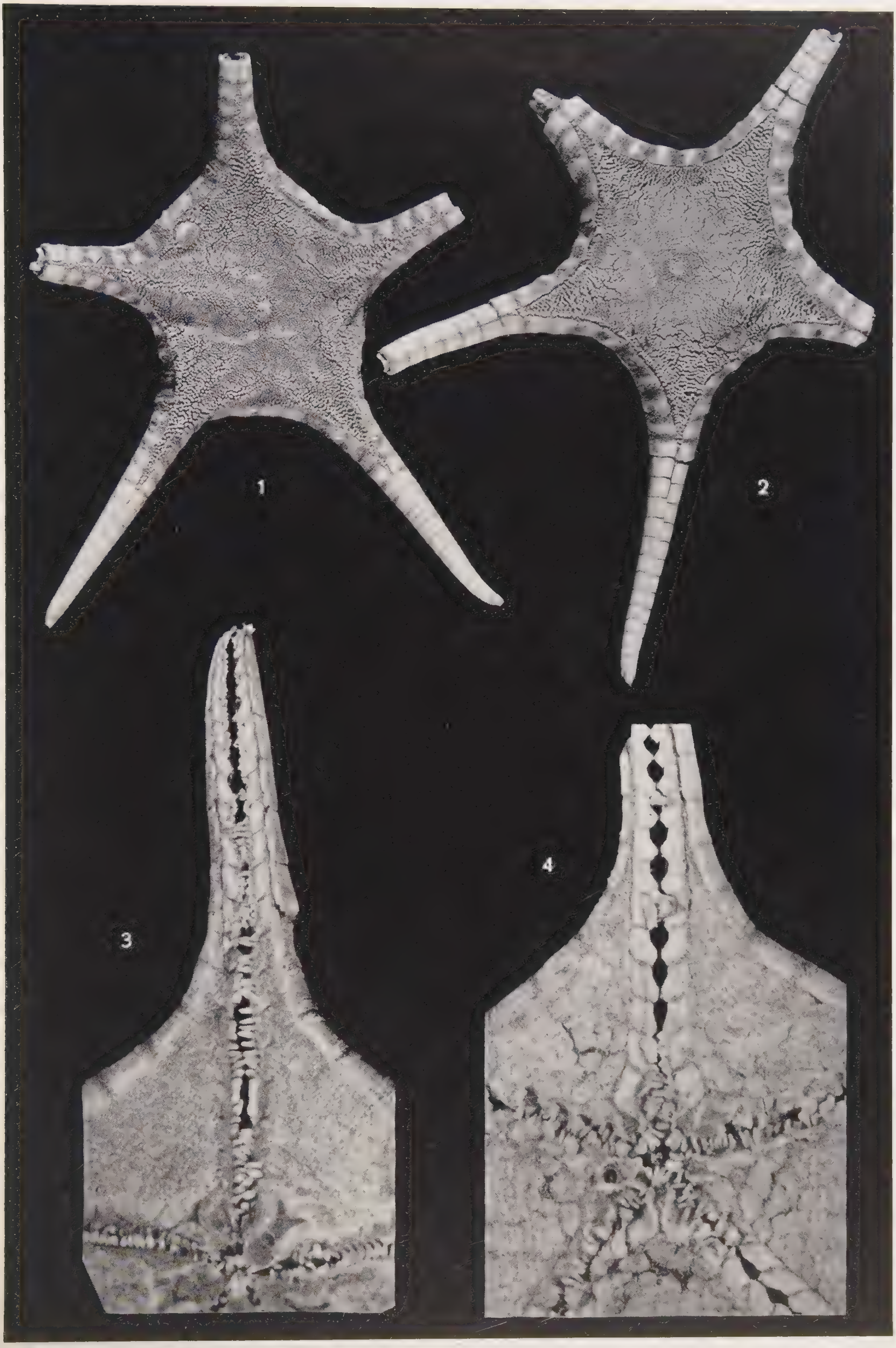

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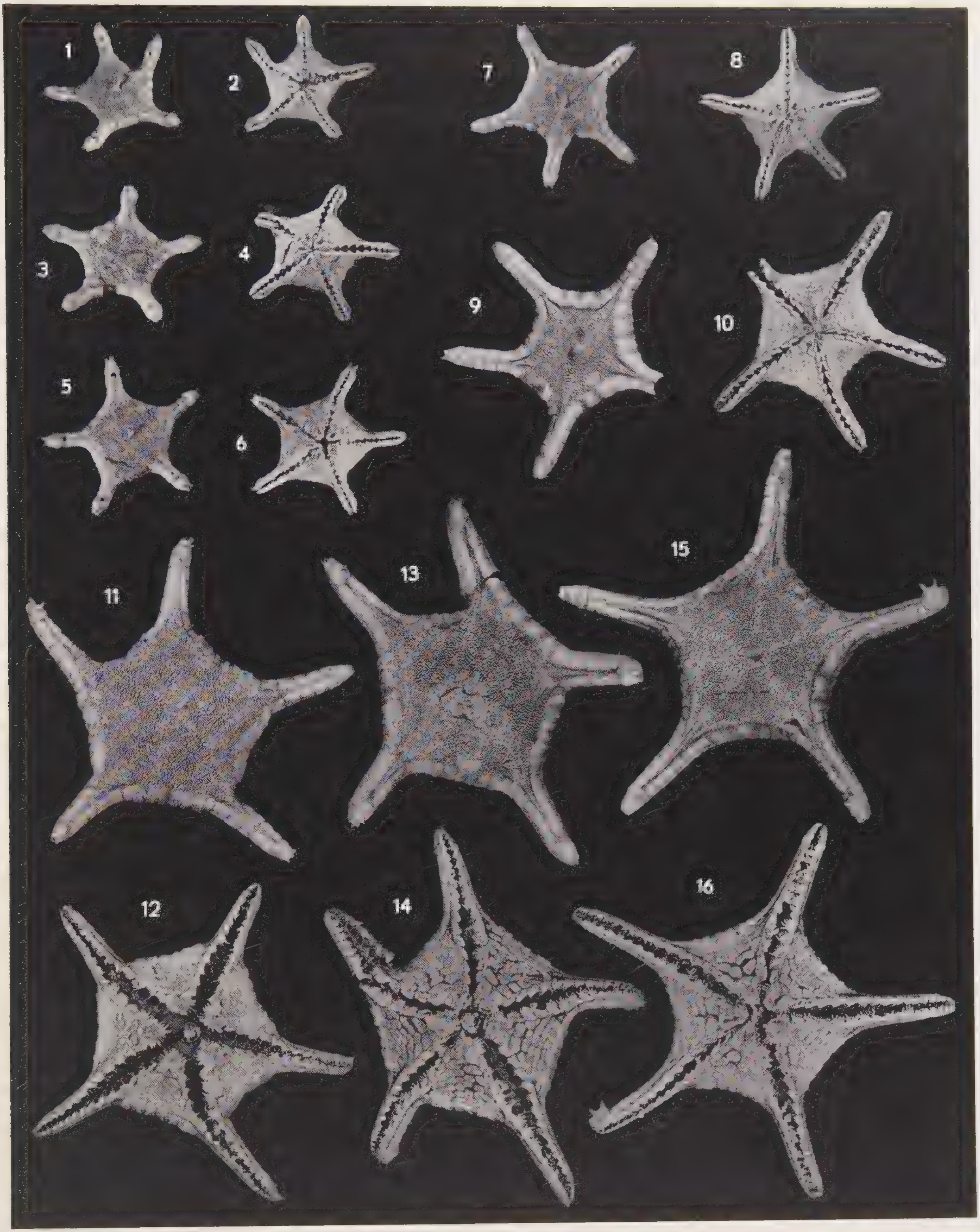
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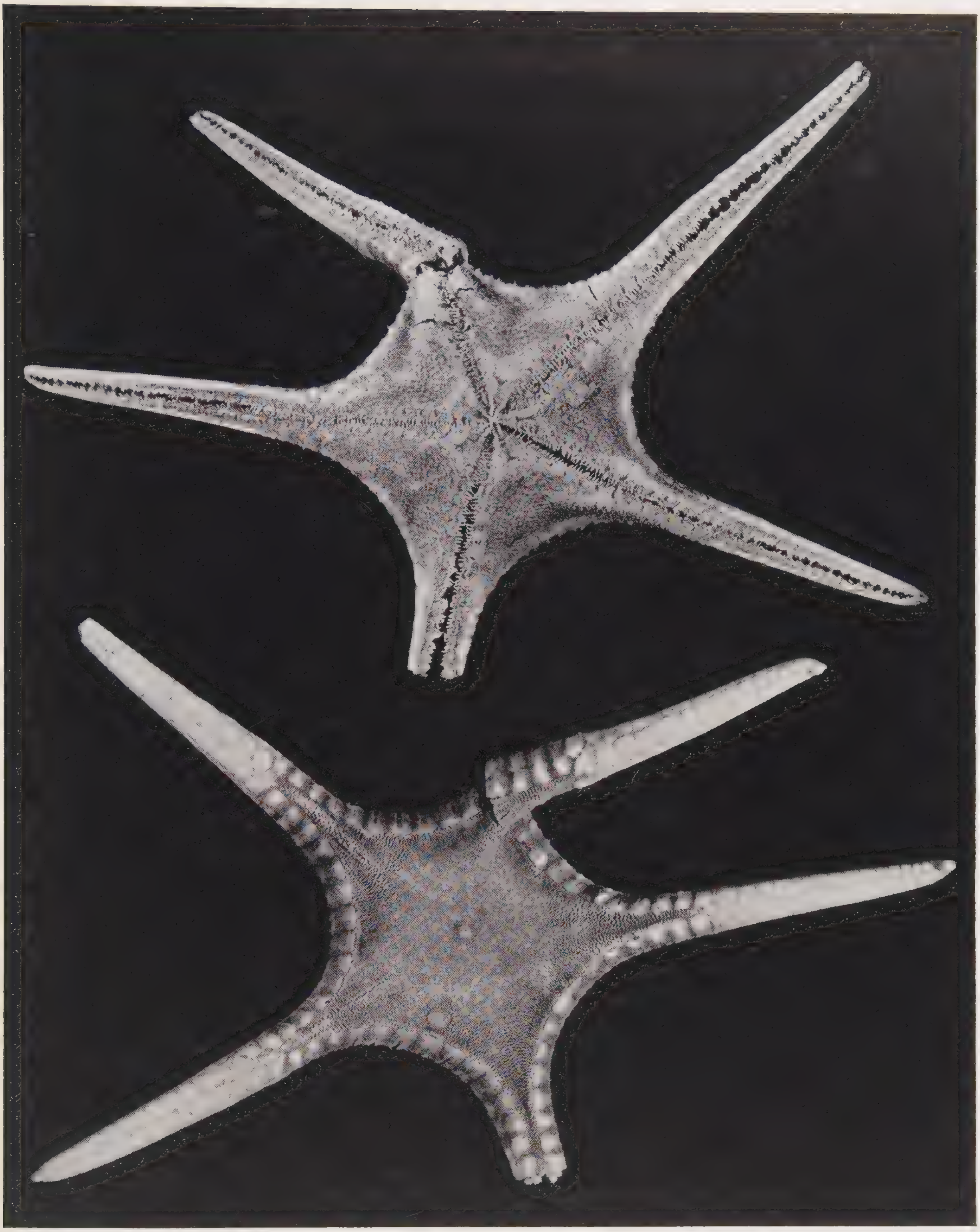

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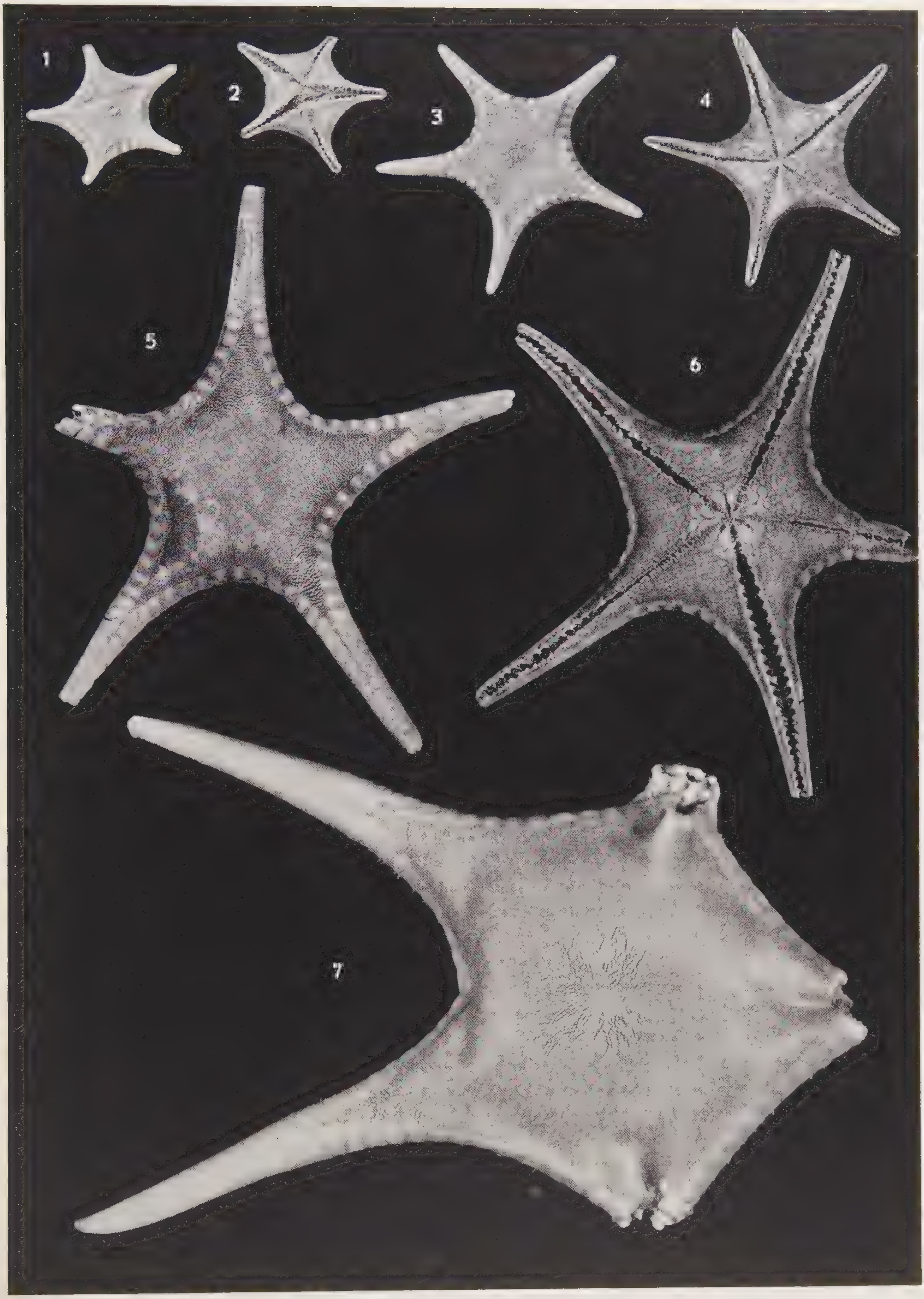

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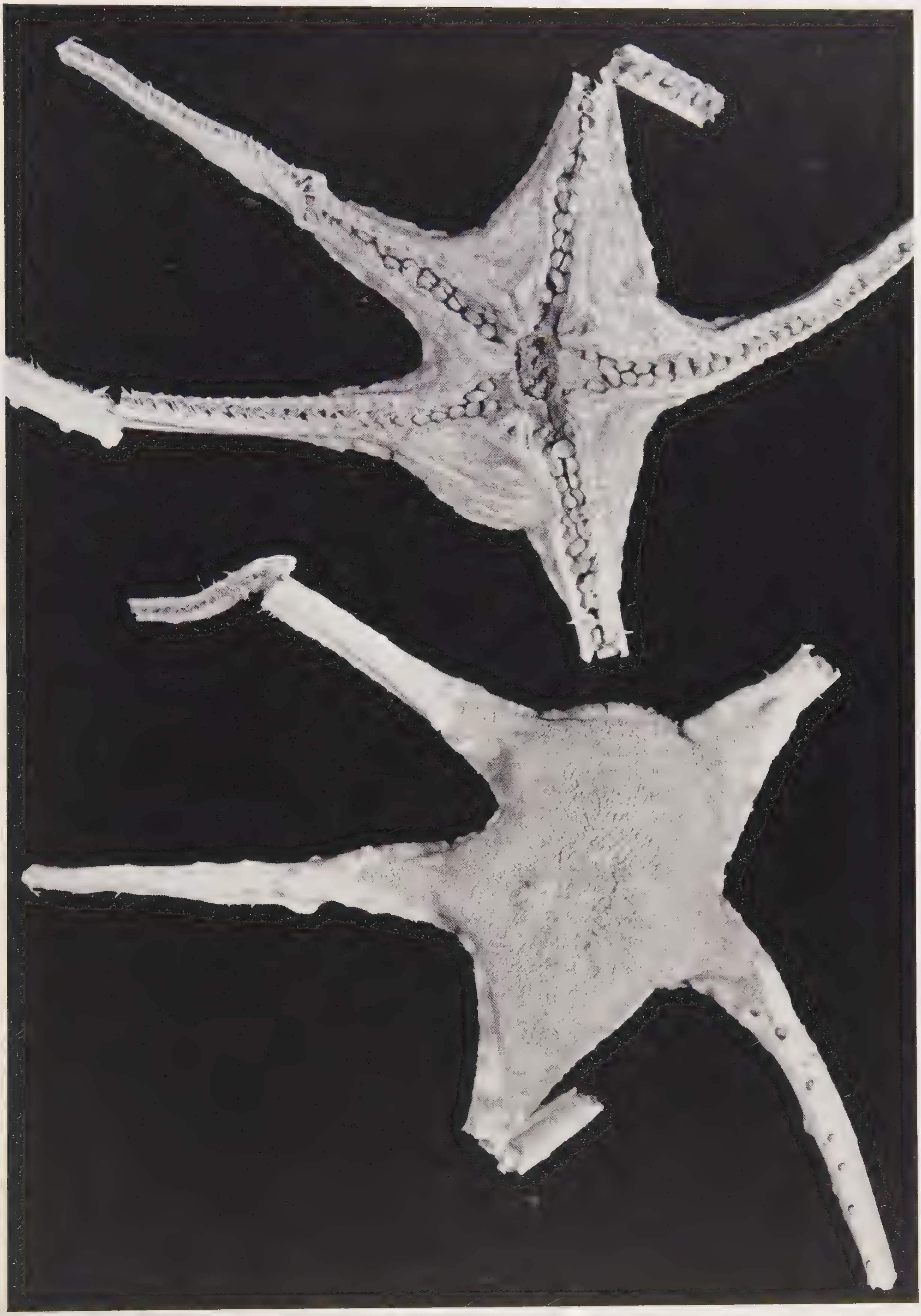

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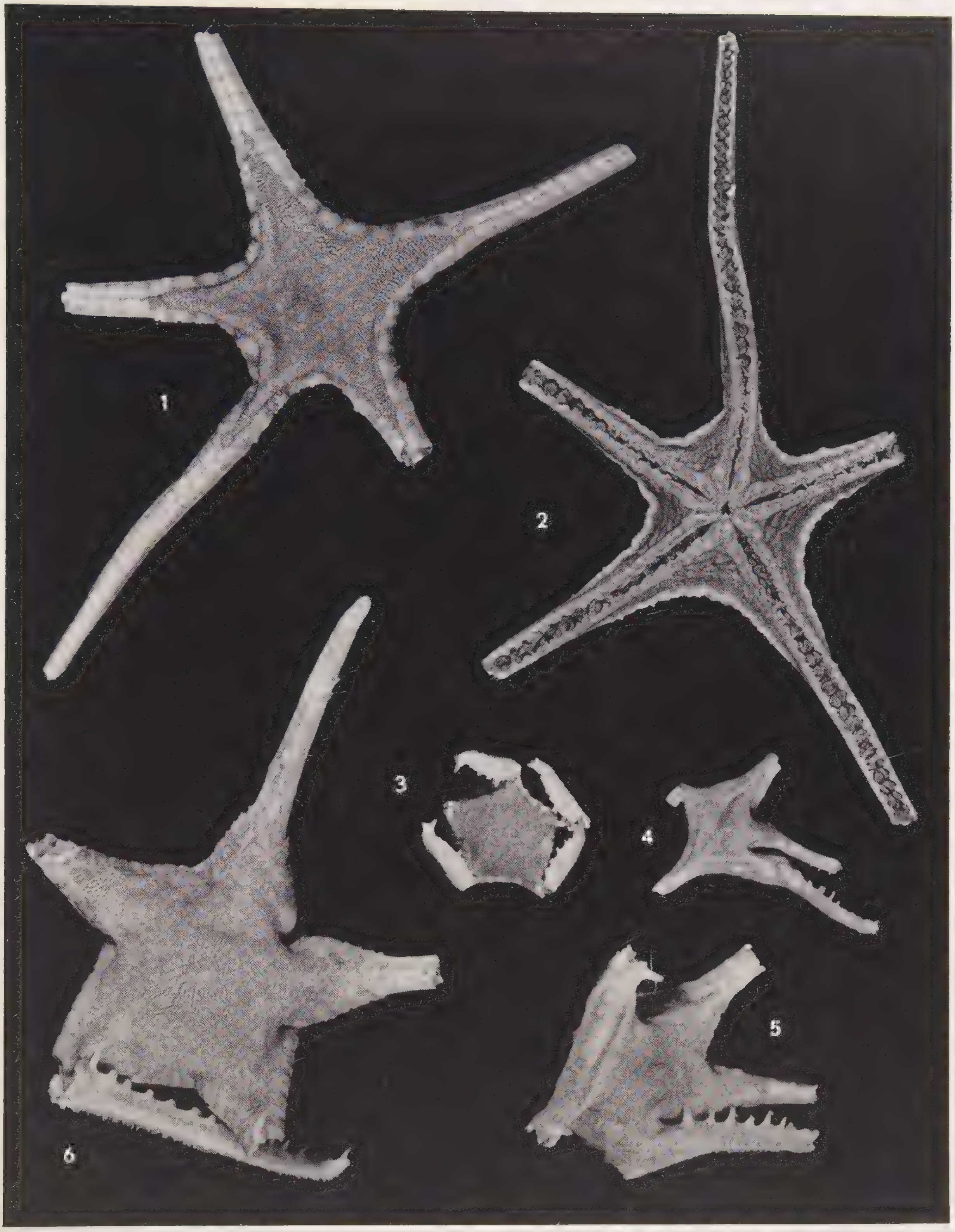

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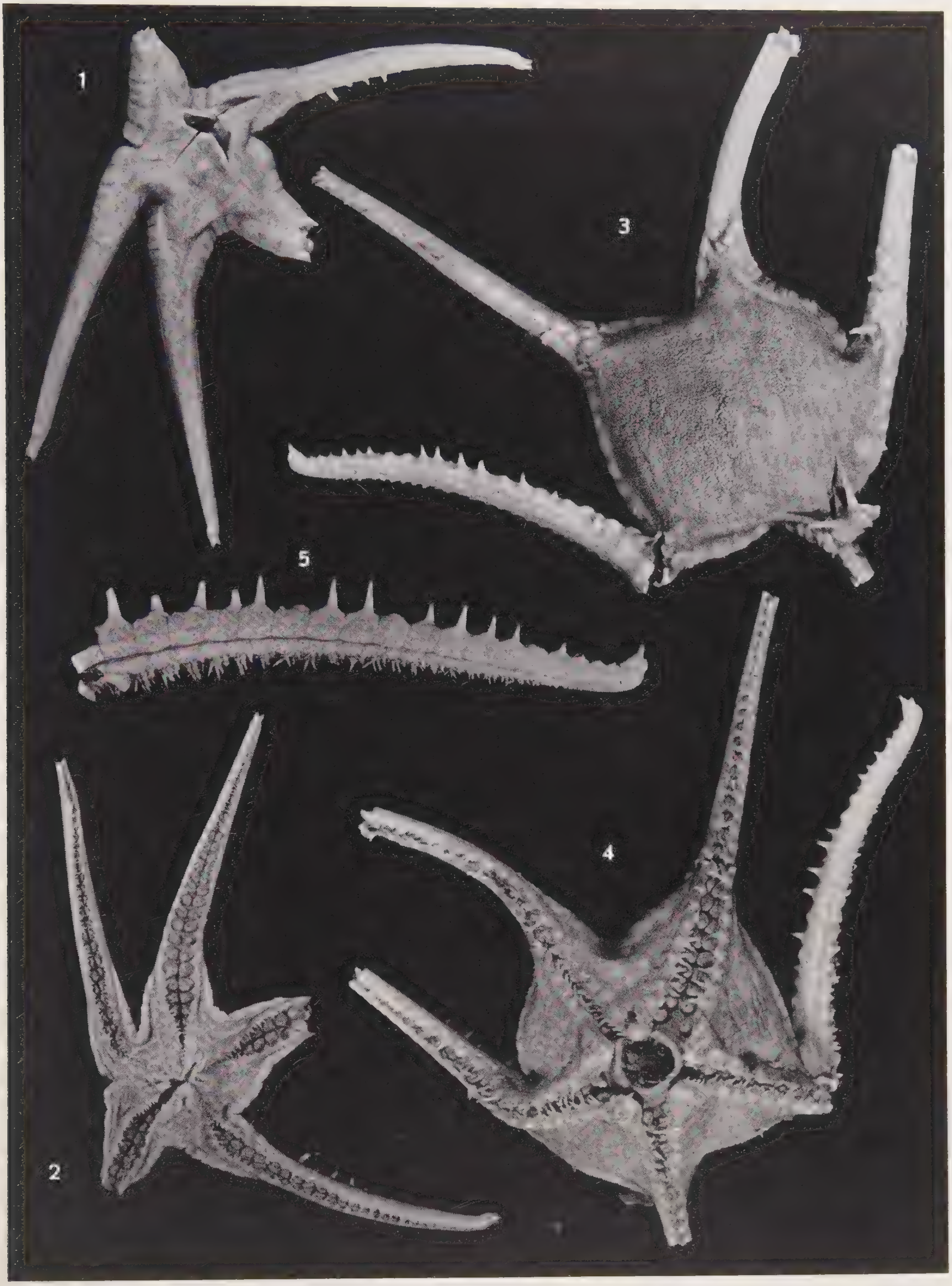

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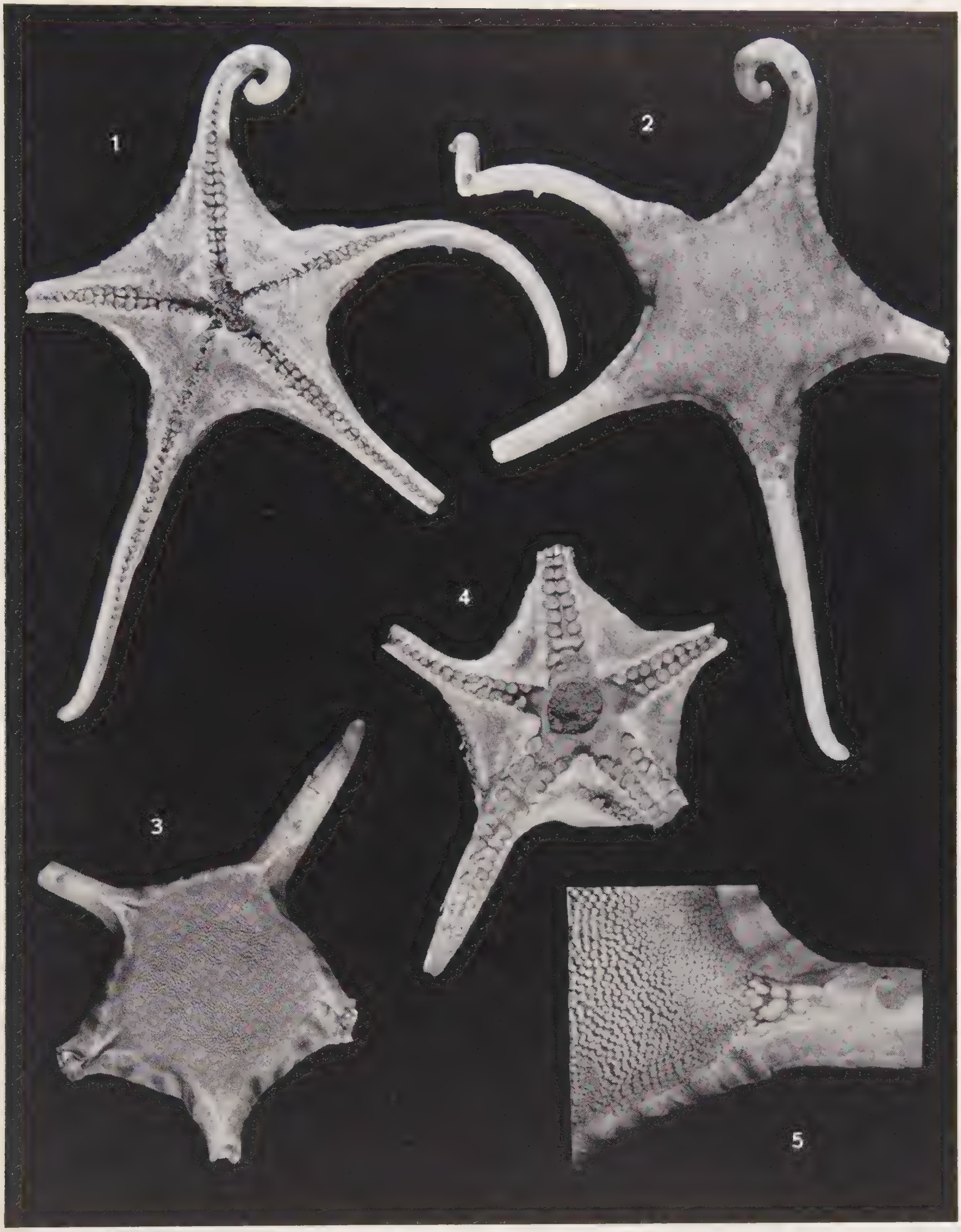

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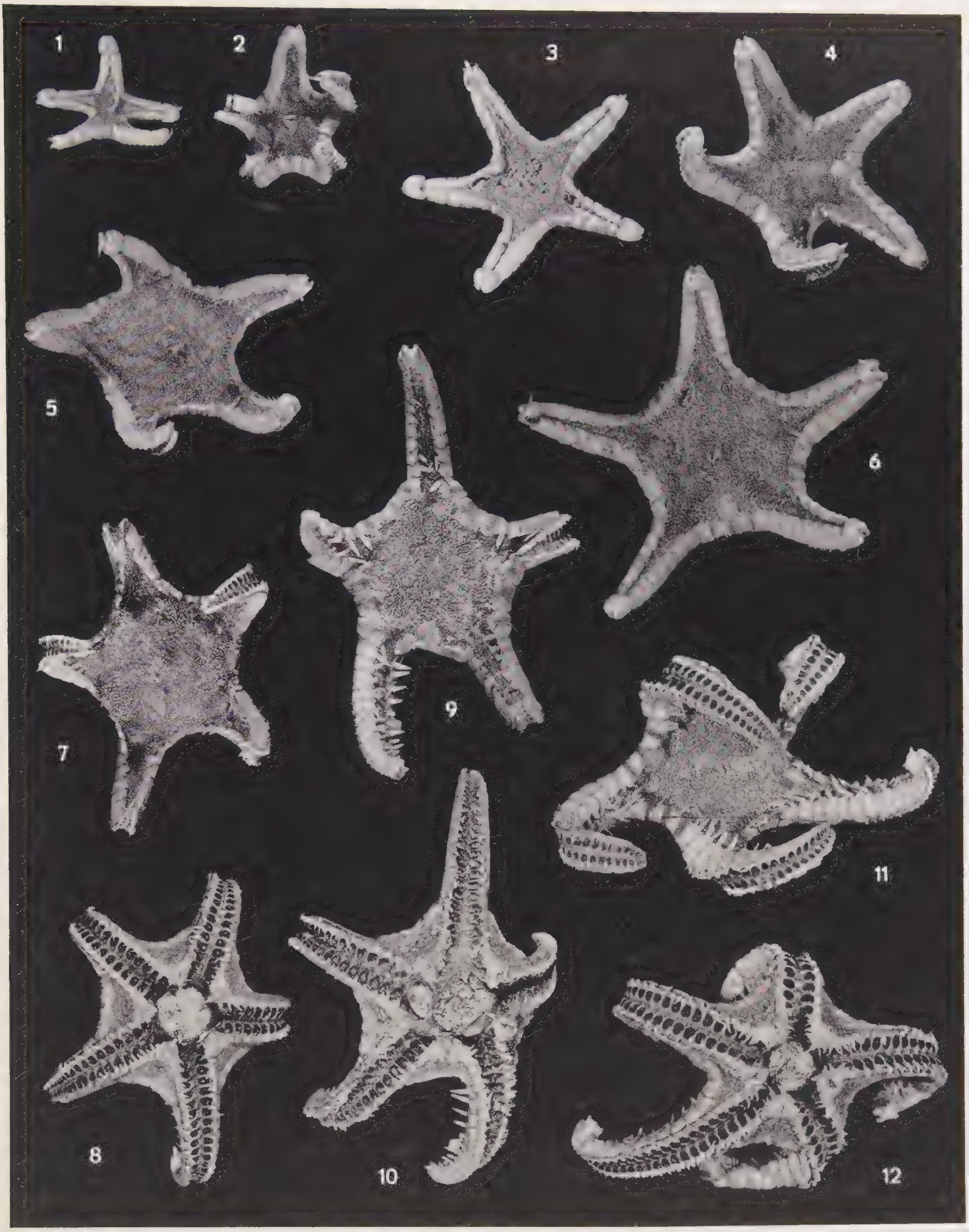

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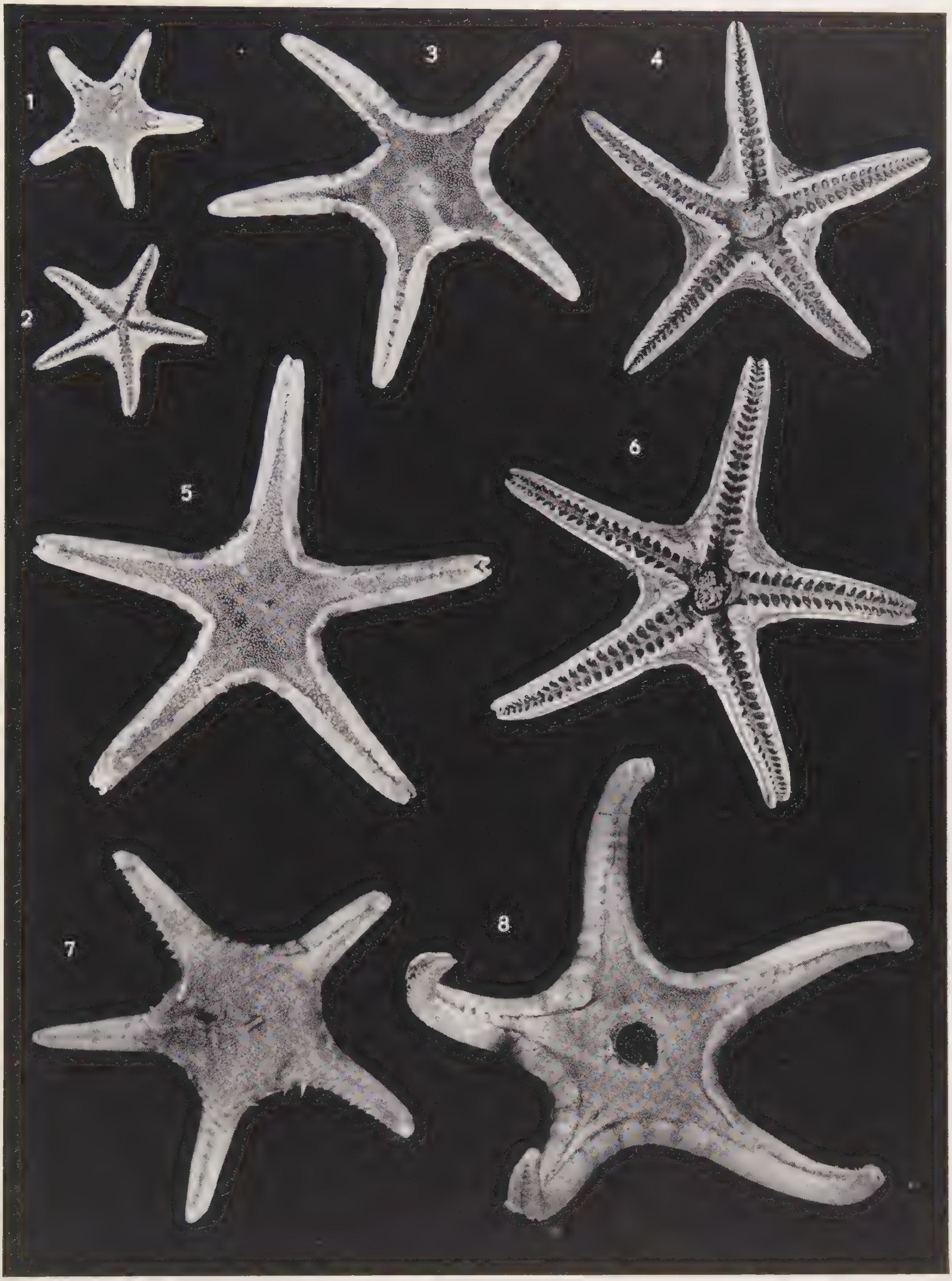

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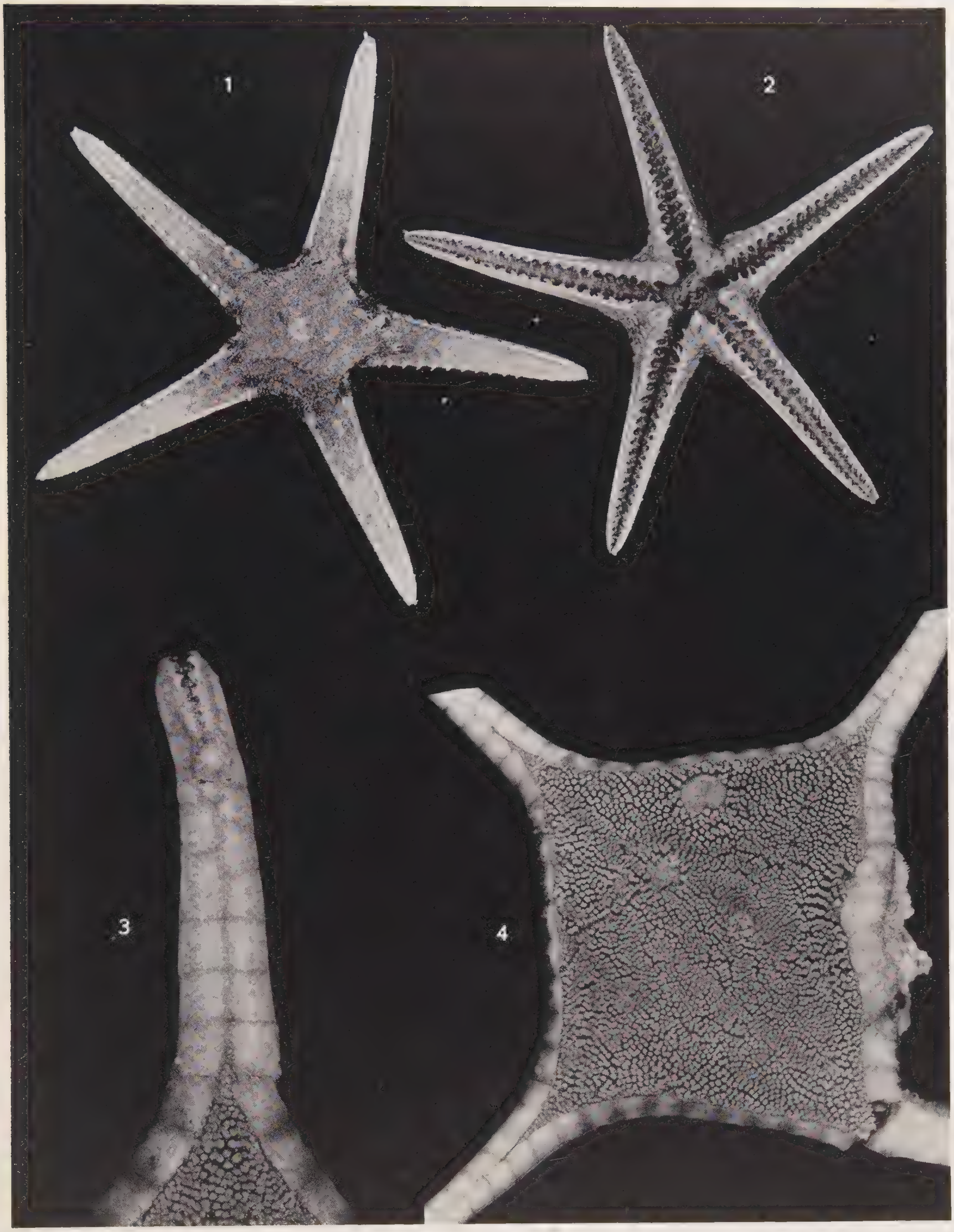

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ON THE ZOOGEOGRAPHY AND ORIGIN OF THE ABYSSAL FAUNA

IN VIEW OF THE KNOWLEDGE OF THE PORCELLANASTERIDAE

By F. JENSENIUS MADSEN
Zoological Museum, Copenhagen

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The writer's English has been revised by Mrs. MANON GOODFELLOW.

I. INTRODUCTORY REMARKS

In his preliminary account of the Challenger Deep-sea Exploring Expedition WYVILLE THOMSON (1877 II p. 328) noted that: "some of the most interesting of the problems which are now before us (after the establishment of the fact that the distribution of living beings has no depth-limit) have reference to the nature and distribution of the deep-sea fauna, and to its relations with the fauna of shallower water, and with the faunæ of past periods in the earth's history." But he thereafter emphasized that: "This is however precisely the class of questions which we are as yet least prepared to enter into, for everything depends upon the careful study and the critical determination of the animal forms which have been procured."

In the following years the results of these studies were published in the scientific report of fifty quarto volumes which provides a permanent record of the Challenger Expedition, and is the starting point for all subsequent taxonomic work on deep-sea animals. Eventually then in 1895 the knowledge collected here, was made use of by MURRAY for a general discussion on the problems of the origin and zoogeography of the fauna of the deep-sea.

The origin of the deep-sea fauna, and the zoogeography of the deep-sea, have, on the whole, been favoured subjects of discussion ever since the existence of a deep-sea life was recognized, and strongly divergent notions have been presented. To some degree, however, apparent incompatibilities may be due to different uses of terminology. Moreover, the problem of the origin of the deep-sea fauna is complicated by this fauna being a mixture of different elements. Further, as regards the zoogeography of the deep-sea, the pattern of distribution may differ in elements of different geological age and perhaps also in different animal groups. A main reason for the difficulties in reaching definite conclusions regarding the problems of the deep-sea fauna, has also been the still insufficient knowledge. More exhaustive collecting is necessary and much more taxonomic work still to be accomplished before a really satisfactory concept of the problems of the deep-sea fauna can be had.

The investigations of the Galathea Expedition Round the World aimed, i.a., at giving us the first knowledge of the fauna of the extreme deep-sea; and it was due to this expedition that we have the ultimate proof of the existence of animal life at all depths. Another remarkable result was the discovery of the Palaeozoic relict, *Neopilina*. However, in the long run the reputation of the Galathea Expedition, as was the case with the Challenger Expedition, will rest on the detailed taxonomic reports on the entire collections, the pains' taking and time-consuming working up of which is now in progress.

The Galathea collections are, from a zoogeographic point of view, of considerable interest, as they offer the taxonomist the rare opportunity of a simultaneous study of materials from widely separated localities. Most other deep-sea expeditions since the Challenger, have collected in more or less limited areas and apparently their collections have sometimes been worked up without much attention being paid to the fauna of other areas. Thus, the taxonomic revision of the deep-sea sea-stars, the Porcellanasteridae, now undertaken on the basis of the Galathea material (see the preceding paper in this report), showed that at most 25 species could be recognized at present, although no less than 57 nominal species have been previously described. Similarly, BROCH recognized only 7 valid species among 39 nominal ones when in 1958 he revised the deep-sea pennatularian genus *Umbellula*. The trend is evident, and at least some increase in the number of synonyms must be expected as a result of taxonomic revisions on comprehensive materials of many other deep-sea groups.

The Porcellanasteridae, which constitute a characteristic element in the abyssal deep-sea fauna, were obtained in a fair percentage of all the dredgings hitherto made in the abyssal depths (e.g. in about one-third of the Galathea dredgings in depths exceeding 2000 m) and at present are among the best known exclusively deep-sea animals as regards taxonomy and distribution (cf. the accompanying table p. 182). It has been found worth-while therefore, on the basis of this knowledge, to review some of the theories set forth on the origin of the abyssal fauna, and on the zoogeography of the abyssal region.

In some earlier papers (cf. p. 204) the writer took up the view that there is a large cosmopolitan element in the abyssal benthic fauna, a view which is corroborated by the now known distribution of the Porcellanasteridae. Further, the amount of evidence now available on the Porcellanasteridae supports the assumption that the recent abyssal fauna in the main is younger than the bathyal and sublittoral faunas.

Even before the investigation of the deep-sea began, many authors had speculated on the possibility of life and the conditions of life in the great depths. Some curious theories were advanced but also some shrewd guesses made. It is not always possible therefore, to state with any certainty who was the first to express this or that idea. In addition, several authors have been known to arrive independently at the same conclusions.

The most valuable of the earlier surveys on the deep-sea fauna is undoubtedly the paper 'On Deep-Sea Dredging and Life in the Deep-Sea', read in 1880 by MOSELEY, one of the Challenger scientists. This paper is quoted more or less directly by most later authors dealing with the subject, and will frequently be referred to in the following pages. Another very important paper on the subject is MURRAY's summary of the scientific results of the Challenger Expedition already mentioned.

II. HISTORICAL STEPS IN THE EXPLORATION OF THE DEEP-SEA FAUNA

The deep-sea was the last of the larger life spheres of the earth to be explored. Up to about 1860 it was generally thought to be lifeless, and this assumption seemed to be confirmed by the researches undertaken by FORBES in the Aegean Sea; the distribution of the animals there (due to the peculiar hydrographic conditions) leading him to the conjecture (1843) that a "zero of animal life would probably be found somewhere about 300 fathoms". It is true that as early as 1819 JOHN ROSS had reported animals obtained from depths down to about 1900 m in Baffin's Bay. This, and other reports of animals brought up with the sounding lines, was overlooked however, or even discredited; it being assumed that the line had coiled up on the bottom or that the animals had been captured while floating near the surface.

WALLICH, who in 1860, in the North Atlantic, had obtained brittle-stars from a depth of 1260 fms (2300 m), published in 1862 a detailed discussion on the possibility of a deep-sea fauna. He stated that the pressure of the vast depths could not preclude the existence of animal life and inferred that, "the deep-sea has its own special fauna, and that it has always had it in the ages past". The final and irrefutable proof of the existence of a deep-sea fauna was, however, the find in 1860 of sessile animals (cf. MILNE-EDWARDS 1861) on a Mediterranean telegraph cable taken up for repair from a depth of about 2000 m.

Animals were collected in abundance in the great depths during the subsequent British explorations of the North Atlantic. Therefore WYVILLE THOMSON (in 1873, p. 31) concluded: "if there be nothing in the conditions of a depth of 2500 fms (4500 m) to prevent the full development of a varied fauna, it is impossible to suppose that even an additional thousand fms would make any great difference". The famous Challenger Expedition 1872-76 brought back rich collections of animals from all oceans and from depths down to 5490 m. A long series of other deep-sea expeditions with more limited scope followed. Prince ALBERT of MONACO's expedition on the Princesse Alice in 1901 made a successful haul (yielding e.g. a porcellanasterid) at a depth of 6035 m, and up to recent years this was the acknowledged depth record for marine life; (the dredging of a siliceous sponge at a depth of 7600 m by the U.S. Albatross in 1899 (A. AGASSIZ 1902 p. 77) usually being overlooked).

It was generally held, however, that the greatest and hitherto unexplored depths would also have a fauna, until some experiments on the resistance of various animals and of cellular tissue to high pressure (FONTAINE 1930) led to the assumption that the increased pressure might be prohibitive to the presence of life at depths below about 7000 m (cf. p. 199). Therefore, although the Swedish Deep-Sea Expedition in 1948 brought up animals from a depth of almost 8000 m, it was only when the Galathea Expedition in 1951 collected animals at a depth exceeding 10.000 m, that the existence of an animal life at all depths in the ocean was conclusively established.

III. THE DELIMITATION OF THE ABYSSAL REGION

The concept of the 'abyssal region' was originally synonymous with the entire deep-sea, i.e. the ocean deep beyond the shelf (and beyond the reach of fishermen), thus, any depth exceeding about 200-400 m. When the explorations of these depths began, it soon became evident however (cf. e.g. E. PERRIER 1899 p. 340), that two main faunistic regions might be distinguished: 1) a lower zone with a sparse and uniform fauna and a very low temperature (to which zone alone the term abyssal is now restricted), and 2) an upper transitional zone (now called the bathyal, or sometimes, the archibenthal zone) with a richer and more varied fauna, and, except for the polar regions, with relatively high temperatures.

The boundary between the abyssal and the bathyal zones can roughly be placed at a depth of about 2000 m, but is set by different authors at 1000 m, 1000 fms, 2000 m, 1500 fms, and 3000 m respectively. These discrepancies, as noted by BRUUN (1957), are partly due to the different position of the 4°C isotherm in different regions; (a temperature of about 4°C being the highest temperature at which the endemic elements in the abyssal fauna are found (cf. p. 198)). – The upper limit of the bathyal zone, or the deep-sea as a whole, similarly depends (as already noted by the Challenger scientists) on the hydrographic conditions in each area. Thus, a deep-sea fauna may be found in the Arctic at depths of perhaps only 30 m, while in western subtropical regions it may not be found until a depth of about 800 m (cf. p. 198). That the temperature adapted for a deep-sea fauna comes nearer to the surface in the tropics than in the temperate zones was pointed out e.g. by A. AGASSIZ in 1888 (p. 164).

The extreme deep-sea (the trenches and deeps), is now considered to constitute a special faunistic region – the hadal (or ultra-abyssal) zone. The upper boundary of this zone (and lower boundary of the abyssal zone) is set at a depth of 6-7000 m.

IV. THE BATHYMETRICAL RANGE OF THE PORCELLANASTERIDAE

All the major marine invertebrate groups have representatives at all depths. Thus the echinoderms (cf. e.g. WOLFF 1960) are represented down to the deepest known depths by the holothurioids and the crinoids (deposit- and suspension-feeders), whereas the ophiuroids are as yet only known to occur down to about 8000 m, the echinoids to about 7250 m, and the asteroids to about 7600 m. Within the Asteroidea, three families, viz. the Pterasteridae, the Brisingidae, and the Porcellanasteridae, reach into the hadal depths. Of these, the Porcellanasteridae are remarkable in being exclusively confined to the deep-sea (no porcellanasterid has hitherto been found at depths of less than about 900 m), and in having their main distribution in the truly abyssal zone, i.e. below a depth of about 2500 m.

Six of the genera of Porcellanasteridae, *Hyphalaster, Abyssaster, Thoracaster, Styracaster, Eremicaster,* and *Porcellanaster* (in all comprising about 20 species), live in the abyssal depths, and only a few of them, *Porcellanaster* and *Eremicaster,* occur also at depths less than about 2500 m, viz. 1200 and 1600 m respectively. (Another species of *Eremicaster* reaches down into the hadal zone, to a depth of

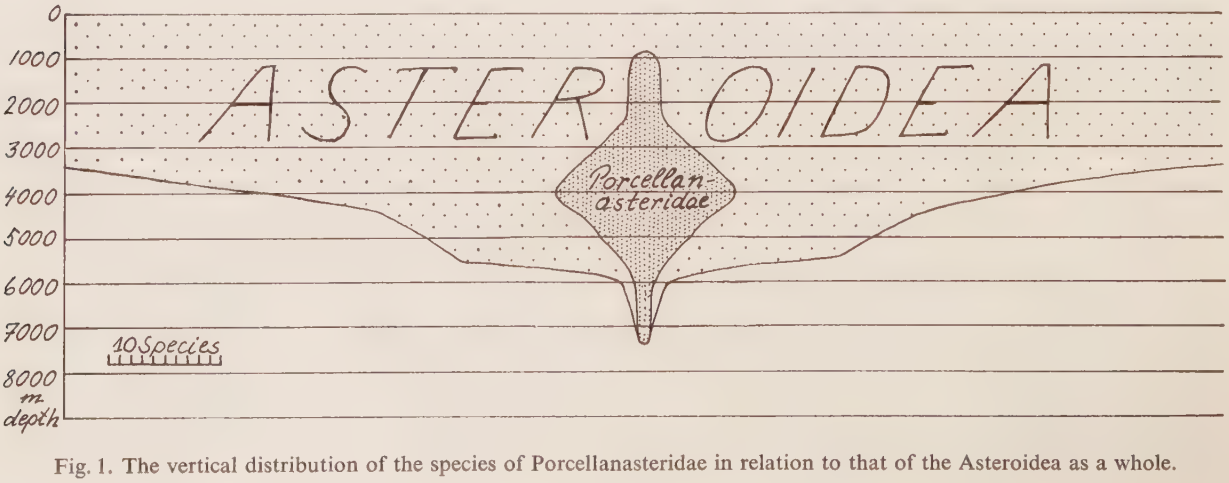

Fig. 1. The vertical distribution of the species of Porcellanasteridae in relation to that of the Asteroidea as a whole.

about 7200 m[1]). The three remaining genera, *Sidonaster, Benthogenia,* and *Lysaster,* which are all monotypic, seem to be exclusively bathyal, being known only from depths between 900 and 2300 m.

The porcellanasterid genera which oceur in the abyssal zone, are known solely from temperatures below about 4°C, and thus seem to be decidedly stenothermal. The bathyal *Sidonaster* seems to be rather eurythermal as it has been found to live at temperatures ranging from 1.8° to 11.3°C. *Benthogenia,* which is known from two localities only, has been found at 9.7° and 11.5°C; and *Lysaster,* known from a single find only, probably lived at a temperature between 6° and 8°C.

V. THE MODE OF LIFE OF THE PORCELLANASTERIDAE

A century ago Wallich noted, in his classical discussion on the presence of animal life at great depths in the ocean, that the deep-sea would be "for ever closed to human gaze". And although the first deep-sea explorers may have visualized it, they could never have seriously considered the possibility of photographing the deep-sea floor, televising the activity there, or of sending a man-manned ship down to the greatest of all depths. These now realized possibilities will eventually give us a reliable knowledge of the life-phenomena in the deep-sea. At present, however, we can still only speculate (albeit with a reasonable degree of certainty) about the mode of life led by the animals there.

The porcellanasterid sea-stars, to judge from their morphological characters and by comparison with knowledge of the mode of life of a related form such as the arctic *Ctenodiscus,* must spend most of their life buried in the soft muddy deep-sea bottom. A very characteristic morphological feature is the so-called cribriform organs (bands of close-set perpendicular cilia-covered folds of skin, or rows of papillae, supported by microscopic 'spines') which are situated on the marginal plates in the arm angles, around the vertical sutures. By means of their ciliary action these organs must serve in producing a circulation of fresh water around the sea-stars in their burrows; a canal being kept open to the surface (to judge from the condition in *Astropecten)* by distention of the usually more or less distinct central dorsal prominence (apical appendage or apical cone).

Like so many other deep-sea animals the porcellanasterids are mud-swallowers or mud-eaters; and presumably they are able, by means of the water currents created by the cribriform organs, to secure and draw down the surface material (which is comparatively rich in organic matter) in order that it may be caught in the mucus secretion and then led to the mouth by the podia. The stomach is a large undivided cavity which fills out almost the entire disk; this latter becoming greatly inflated when the stomach is well filled with bottom material. There is no intestine and anus; thus, after the organic matter has been utilized, the stomach content has to be emptied out through the mouth opening. This can be greatly expanded, and it would seem that the porcellanasterids besides being deposit-feeders, may be scavengers and facultative predators.

The gonads are small, even when ripe, consisting merely of a few branched tubules, not much longer than the height of the marginal plates where they are closely juxtaposed. The ripe eggs measure 0.5-0.6 mm in diameter which confirms an expected non-pelagic development. Individuals with ripe gonads have been found with the stomach well filled, which would indicate that the reproductive phase is not accompanied by any pause in feeding activity. The available samples of populations further include individuals with unripe gonads besides those with ripe ones, agreeing with the assumption of a sporadical reproduction within the populations.

A commensal hydroid has been found living on *Eremicaster*, and is usually attached to the ventral side of the sea-star, especially in the region around the mouth. The porcellanasterids are also fairly frequently infested with dendrogate ascothoracids, and with myzostomes.

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[1] Dr. G. M. Belyaev has kindly informed the writer that a specimen of *Porcellanaster* was collected at 7584-7616 m in the northern part of the Mariana Trench, during the recent Russian explorations of the Pacific deep-sea.

Table 1. Survey of the geographical and bathymetrical distribution of the Porcellanasteridae.

	Number of finds in						Temperatures recorded in C°	Bathymetrical range	Total number of records	Number of finds in							
	Atlantic Ocean	Indian Ocean	Malayan region	Pacific Ocean						900 –1000 m	1000 –2000 m	2000 –3000 m	3000 –4000 m	4000 –5000 m	5000 –6000 m	6000 –7000 m	7000 –8000 m
				West	mid	East											
Hyphalaster hyalinus					1		1.7°	5030 m	1						1		
Hyphalaster inermis	20	8		3	1		1.1°-3.9°	2278-5413 m	32			7	11	9	5		
Hyphalaster giganteus		1						ab. 3850 m	1				1				
Hyphalaster scotiae	(1)							2580 m	1			1					
Lysaster lorioli		1					ab. 6°-8°	≧ 1000 m	1		1						
Benthogenia cribellosa			1				9.7°-11.5°	905-925 m	1	2							
Abyssaster tara		7		1			1.1°-1.8°	3200-6280 m	8				6	1		1	
Abyssaster diadematus						1	1.8°	3950 m	1				1				
Abyssaster planus		(1)					0°	3566 m	1				1				
Thoracaster cylindratus	6	8		1		5	1.3° 2.8°	2600-ab. 5000 m	20			3	5	12			
Styracaster horridus	9	4		2			1.1° 2.4°	4040-5610 m	15					9	6		
Styracaster caroli		6					1.7° 2°	2600-4820 m	6			3	2	1			
Styracaster elongatus	5	2						3310-4870 m	7				3	4			
Styracaster chuni	4			2			1.1°-3.9°	2550-ab. 4550 m	6			3	1	2			
Styracaster paucispinus						1	1.8°	4335 m	1					1			
Styracaster robustus	(1)							3846 m	1				1				
Styracaster armatus		3		1			1.3°-1.9°	3365-4350 m	4				3	1			
Styracaster spinosus	5							2995-4360 m	5			1	2	2			
Styracaster clavipes		1					1.7°	3197 m	1				1				
Styracaster monacanthus						1	1.9°	4143 m	1					1			
Porcellanaster cæruleus	69	8	3	3		3	1.1°-4.2°	1158-6035 m	86*		15	17	6	4	1	1	
Eremicaster crassus		4			1		1.2°-1.8°	3390-4271 m	5				4	1			
Eremicaster gracilis				5		18	1.3°-2.6°	2690-5204 m	23			3	9	8	3		
Eremicaster pacificus				[1]		14	1.6°-2.9°	1571-4088 m	15**		4	5	4	1			
Eremicaster vicinus	1	1		3		2	1.3°-2.4°	5204-ab. 7200 m	7						3	3	1
Sidonaster vaneyi		11	6				1.8°-11.3°	1147-ab. 2300 m	17		13	3					

* The survey of the bathymetrical distribution of *Porcellanaster cæruleus* considers only 44 finds; exact information of the 42 finds made by the Albatross 1883-84 in the N. W. Atlantic, in depths of 1657-3520 m, not being available.

** The depth of one find is unknown.

() The finds in question were made in the Antarctic region.

[] The find was made in the Bering Sea.

VI. THE GEOLOGICAL AGE OF THE PORCELLANASTERIDAE

When summarizing his considerations on the Porcellanasteridae SLADEN (1889 p. 126) noted that in some respects they "appear to present a more archaic character than the Archasteridae", but that this seemed to him to be "dependent on striking features of structural detail rather than on general fascies". He further noted that the apparently archaic fascies was "largely due to the remarkable degree in which the Porcellanasteridae present permanently characters which are regarded, in the majority of forms at least, as essentially embryonic". Probably SLADEN had in mind the large terminal ossicles, the large marginal plates, and perhaps also the apical appendage.

FISHER in his Monograph of the Asteroidea of the North Pacific (1911-30) grouped the families, as closely as a linear arrangement would permit, in what seemed to him the most natural order. The Porcellanasteridae he placed first however, not because they were conclusively considered the most primitive, but (1911 p. 4) in order "to avoid sandwiching them between the Astropectinidae and some other family, and because they stand apart from the other Phanerozonia". (FISHER recognizes within the Asteroidea the three main groups: the Phanerozonia, the Spinulosa, and the Forcipulata). In 1928 he called the Porcellanasteridae "archaic though highly specialized".

It is the typical phanerozoniate sea-stars, such as *Astropecten* and allies, which FISHER and several other authorities on sea-stars (e.g. SLADEN, LUDWIG, DÖDERLEIN, KOEHLER, MORTENSEN, and SPENCER) regard as being the most primitive of the recent forms. However, other authorities (e.g. E. PERRIER, GEMMILL, and MACBRIDE) consider these sea-stars highly specialized, and regard the Spinulosa as the most primitive.

MACBRIDE (1923), when criticizing the concept of the primitiveness of the Astropectinidae, says somewhat sarcastically that the systematists holding this view are "– for the most part – students of the external features of preserved specimens only". He notes that "what these specialists are impressed by is the 'phanerozoniate' character of the Astropectinidae, that is the edging of the arms with a series of broad plates termed the 'marginals'"; and then goes on to critizise this view, claiming that the apparent marginals of the ancient starfish "are not homologous with the marginals of the modern Paxillosa (i.e. *Astropecten* and allies) at all but are the adambulacrals". – The writer should like to point out, however, that although this argument was allowed to stand, it does not hold. True enough, in some types of Palaeozoic sea-stars (e.g. the Ordovician *Cnemidactis)* the adambulacral ossicles are very large and appear along the sides of the arms as a series of inferomarginals, but in other Palaeozoic sea-stars (e.g. the Ordovician *Hudsonaster)* the adambulacral skeleton only bounds the furrows, whereas the arms are armed laterally with genuine marginal plates. Thus, MACBRIDE's criticism cannot refute the concept of the phanerozoniate sea-stars being the most archaic type.

It appears however, taking everything into consideration, that the question of which recent group of sea-stars is the most primitive in existence, is an unanswerable one. The knowledge of the earliest types of sea-stars does not seem to offer any clue to the interrelationships of the later ones. The early Palaeozoic star-shaped echinoderms, which are placed in the classes Asteroidea and Ophiuroidea, are actually so different from the modern types, that it has even not always been immediately evident to which of the two classes, certain of the Palaeozoic forms belonged. Palaeozoologists therefore also generally place the Asteroidea and the Ophiuroidea in a common supergroup, the Stelleroidea. In some modern works (e.g. HYMAN 1955) it is maintained, however, that the Ophiuroidea are more closely related to the Echinoidea than to the Asteroidea. This view is based, among other things, upon the similarity in the general appearance of the larvae of the Ophiuroidea and the Echinoidea, and upon the occurrence of the same type of sterols in some biochemically tested ophiuroids and echinoids, and a different type in the asteroids (cf. BERGMANN 1949). However, the palaeozoological and morphological evidence (cf. SPENCER 1914-40) supports equally well the concept of a closer relationship between the Asteroidea and the Ophiuroidea than between the Ophiuroidea and the Echinoidea. But taken together these three groups stand apart from the other recent echinoderms, the Holothurioidea and the Crinoidea.

The possession of the so-called cribriform organs makes the Porcellanasteridae a highly specialized group among the paxillose phanerozoniate sea-stars. The group is also in some other characters distinct from its nearest relatives within the Phanerozonia, i.e. the Goniopectinidae and the Astropectinidae. It seems justified, therefore, to consider the Porcellanasteridae as a special suborder, the Cribellosa, as did FISHER in 1911.

In the writer's opinion the Porcellanasteridae may be roughly estimated to have split off from the common astropectinid stock in Late Mesozoic, if one judges from the rate of evolution ascertained through fossil evidence in some other groups (e.g. in the echinoids which are so well known through TH. MORTENSEN's monograph, 1928-51). A support of this assumption may also be the fact that the geological age of the recent non-endemic abyssal fauna elements, to judge from the Palaeontological evidence, is similarly Late Mesozoic (at the earliest).

The marginal plates of the Porcellanasteridae have the cribriform organs typically developed on more or less marked depressions which show distinctly on the plates when the papillae in the organs are removed. Possible fossilized marginal plates of porcellanasterid sea-stars, should therefore, be very easy to recognize. No fossil porcellanasterids are known however, and though one cannot rely on negative palaeontological evidence, this nevertheless may be mentioned as a fact consistent with the exclusive deep-sea occurrence of the group (the origin of all fossil marine faunas being shallow water or moderate depths at most). The absence of fossil porcellanasterids supports the assumption that the group has evolved within the deep-sea, i.e. that the complicated cribriform organs were not acquired by their astropectinid-like ancestors until after they had become deep-sea dwellers (see further p. 200).

Because of their embryonic characters the writer suggests that the evolution of the Porcellanasteridae has been brought about by the phenomenon which GARSTANG (1922) designated as paedomorphosis (i.e. by a delayed morphological development along with a gradually accelerated sexual maturing, or in other words with embryonic characters moved into the fullgrown stage).

VII. THE INTERRELATIONSHIPS OF THE PORCELLANASTERID GENERA

The nearest relatives of the Porcellanasteridae are the Goniopectinidae and the Astropectinidae, and it is probable that these three groups have arisen from a common astropectinid-like stock. Astropectinid-like sea-stars are known from the Jurassic, and true astropectinids from the Cretaceous (cf. e.g. DURHAM & ROBERTS 1948) while the goniopectinids, like the porcellanasterids, are without fossil records. The recent astropectinids have a world-wide range and also include several abyssal forms, but otherwise have their chief development in the tropical sublittoral and bathyal regions. The Goniopectinidae show close similarities to the Porcellanasteridae and may have split off from the common astropectinid stock along with this group. However, they are less specialized and are entirely confined to the sublittoral and bathyal depths.

The porcellanasterid genera may roughly be divided into two groups (fig. 2):

1) A larger and somewhat heterogeneous group comprising the most primitive genera, *Lysaster* and *Benthogenia,* as well as *Hyphalaster* and *Thoracaster* (a simple adambulacral armature and in general many cribriform organs) plus the more specialized and thus phylogenetically younger *Styracaster* and *Abyssaster* (smaller number of cribriform organs, possibly a more specialized oral and adambulacral armature, and, in the case of *Styracaster,* a specialized arm-armature).

2) A homogeneous group of probably young phylogeny (with few cribriform organs and a more or less specialized oral and adambulacral armature) comprising *Sidonaster, Eremicaster,* and *Porcellanaster.* (The forms in this group may have evolved from primitive porcellanasterids by a further paedomorphosis (cf. above)).

Two primitive members of the first group, *Lysaster* and *Benthogenia,* are confined to the bathyal zone, being known from depths of 900-1000 m. *Hyphalaster* and *Thoracaster* have a known range of 2275 to 5410 m, and of 2600 to 5000 m, respectively. *Styracaster* ranges from 2550 to 5610 m, and *Abyssaster* from 3200 to 6280 m. The four latter genera are thus confined to the truly abyssal zone.

One of the genera in the second group, *Sidonaster,* is exclusively bathyal, ranging from 1150 to 2300 m. The other two, *Porcellanaster* and *Eremicaster,* have the widest bathymetrical range of all the porcellanasterid genera, viz. 1160 to 6035 m, and 1570 to about 7200 m, respectively. Thus, it is the presumably younger types of porcellanasterids which have penetrated into the greatest depths.

The two supposedly most primitive genera of the Porcellanasteridae, *Lysaster* and *Benthogenia,* belong to the bathyal zone in the tropical Indo-Malayan region, where on the whole the greatest number of genera occur. Thus this region might be considered the center of creation of the Porcellan-

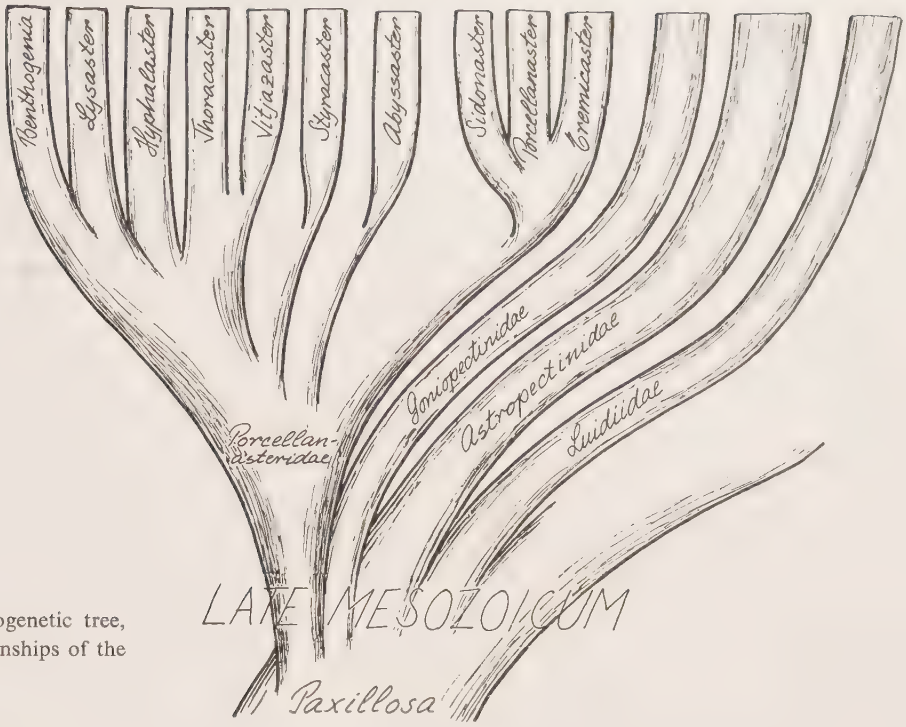

Fig. 2. Suggestion of a phylogenetic tree, showing the supposed relationships of the recent Porcellanasteridae.

asteridae, as has also been the assumption with regard to several other animal groups. However, as will be touched upon in the following (p. 211) this reasoning is probably not sound, the faunal richness rather being due to the fact that the ecological conditions during the Tertiary and Quaternary periods have remained more stable in the Indo-Malayan region than in most other regions of the ocean.

The older types of abyssal porcellanasterid genera, *Thoracaster* and *Hyphalaster,* comprise only one and a few (3) species respectively, and both *Thoracaster cylindratus* and *Hyphalaster inermis,* which are abundant in individuals, show rather fixed taxonomical characters. A younger type, such as *Styracaster,* is split up into a fairly large number of species (10). *Eremicaster,* another young type, is split up in two or three species showing evidence of somewhat unstable taxonomical characters. *Porcellanaster,* probably the youngest abyssal generic type, is monotypic but polymorphic.

VIII. THE GEOLOGICAL AGE OF THE DEEP-SEA

Some of the first deep-sea biogeographers, e. g. Wyville Thomson and Murray, were of the opinion that a continuous deep ocean had existed since early Palaeozoic times. Other authors, however, have expressed quite different opinions as to the age of the oceans. Some have even considered that they were formed as late as Jurassic times, and others have considered the Pacific an ancient and permanent feature of the earth's crust, while they assigned a youthful development to the Indian and Atlantic oceans. The prevailing opinion now seems to be that of the permanency of the oceans.

The land and ocean masses, according to such theories as those set forth by Vening-Meinetz (1944), and Hills (1947) (see Kuenen 1950), were in the main already formed when the crust of the earth hardened (the present distribution of the land masses being remarkably similar to the distribution which is arrived at on purely theoretical grounds when considering the action of convection currents on the masses of a cooling earth). The great oceans according to these theories thus constitute a primitive feature of the earth's crust and may never have been subject to any drastic changes, but only to changes connected with the elevation or subsidence of continental marginal areas, isthmian links and island festoons.

"It is important to note," says Kuenen (1950 p. 130) when summarizing his considerations on the geological history of the oceans, "that, since as far back as the Cambrian, at least, the upper surface of the continents has been close to sea level, just at it is at present, being sometimes partly flooded, sometimes laid almost dry."

IX. LIFE CONDITIONS IN THE ANCIENT AND IN THE RECENT DEEP-SEA

Life in the deep-sea, because of the absence of sunlight, is totally dependent upon the supply of organic matter from land and from the upper lighted water layers. In the first case the organic matter is washed out into the sea by the rain water (together with enormous quantities of inorganic material), or carried out over the sea by the wind; and the land-derived material which is deposited on the bottom near land (the terrigeneous deposits) then may be transported far into the ocean by mud flows or turbidity currents. In the second case the organic matter is basically produced through the photosynthesis of the phytoplancton, and then transferred to the deep-sea via the dead remains of the pelagic plants and animals sinking, or by animals actively descending.

Essentially the deep-sea is, and has always been, a very calm milieu. Very small particles, inorganic and organic, may settle on the bottom, and this is consequently covered with a very soft substratum. (However, on the bottom far from land (with eupelagic deposits) in the areas with a low productivity in the upper water layers, the intensity of sedimentation may be only 0-0.4 cm per 1000 years (cf. Arrhenius 1950 p. 86).)

The biomass (i.e. the quantity of substance in live organisms, or total standing crop, in grams per square meter) is extremely small in the deep-sea in comparison with that in the shallow coastal areas. Near the shore, in depths of 50 m e.g., the biomass may exceed 1000 gr/m^2 (cf. Barnard 1959), and 500 gr/m^2 is a common figure in richer sublittoral-upper bathyal areas. With increasing distance from land and with increasing depth the biomass diminishes rapidly, however. In the abyssal depths ($>$3000 m) in Antarctic and sub-Antarctic regions, and in the offshore regions of the boreal Pacific e.g., the biomass is of a magnitude of 0.8-0.5 gr/m^2. In the tropical open oceans (on the eupelagic deposits) it is on average 0.08 gr/m^2 in the Pacific and 0.03 gr/m^2 in the Indian Ocean (cf. Belyaev 1959), and in the trenches far from land it is still smaller (e.g. in the Tonga Trench, in 10.500 m, only 0.001 gr/m^2 (cf. Birstein 1959)).

In accordance with their opinion that there had been a continuous deep ocean from Silurian times to the present day, Wyville Thomson and others also assumed that there had always been an abyssal life. Since, however, the deep-sea dredgings of the Challenger, contrary to anticipations, did not bring up representatives of a decidedly ancient fauna, Moseley (1880), A. Agassiz (1888), and Murray (1895), advanced the view that the deep-sea had been uninhabitable to a higher life during the whole or most of the Palaeozoic era, and that its fauna dated back no further than the Cretaceous.

Moseley (1880 p. 591) offered as a rather vague explanation of a lifeless Palaezoic deep-sea that it had been overcharged with various gases, salts and mud, whereas Murray (1895 p. 1439) suggested that it had been anaerobic because a vertical circulation between the deep waters and the oxygenated surface waters was prevented by the conditions of the temperatures, which he assumed were fairly high and universally uniform. – According to this latter assumption a deep-sea life did not become possible until Late Mesozoic, when the poles began to cool off, and cold, dense and oxygenated waters descended to the greater depths.

Oxygen can be added to the ocean only in the upper water layers, by the absorption of air and the photosynthesis of plants. Thus the deep-sea region is entirely dependent on the continuous supply of oxygenated water-masses for its content of oxygen.

Some recent water-masses have been estimated, on the basis of measurements of the C14 activity, to be almost 2000 years old (cf. Suess et al. 1959), and if they remain stagnant they will eventually become anaerobic. It is possible, therefore, that there have been large stagnant and anaerobic water-masses in the depths during earlier geological periods. On the other hand this can surely never have been a universal feature, since at least some vertical circulation must have been maintained through those differences of the surface waters of the high and low latitudes which, however slight, must have existed at all times on account of the different solar radiation. – In the recent oceanic bottom waters the amount of oxygen is on an average 5-6 cc/l in the Atlantic, and somewhat less, e.g. 3.5 cc/l, in the Pacific (cf. e.g. Richards 1957).

One of the primary characteristics of the recent abyssal deep-sea is its constant and very low temperatures (0-2°C), which are conditioned by the extremely cool water-masses sinking down in the polar regions and from there streaming over the bottom towards the equator. This characteristic was probably acquired in fairly recent geological times, since during the Mesozoic and earlier Tertiary the abyssal waters must have been warmer; the temperatures at the poles being higher than now, and the vertical circulation more effective on account of the relatively higher density of the polar surface waters when not diluted by melting glaciers (Simpson 1940). – At present the time required for the surface waters to reach, from e.g. the Antarctic to the equator along the bottom, may be from 10 to 30 years (cf. Dietrich 1957 p. 395).

It is the very similar Triassic and Jurassic marine shallow water faunas, including coral reefs, known from high as well as from low latitudes (cf. e.g. Neaverson 1955, Müller 1959), which imply that the ocean temperatures during earlier Mesozoic periods were fairly equable all over the globe, or at least, rather high in the higher latitudes of the northern hemisphere. (This is on the assumption that the ecology and tolerances of temperatures of the coral reefs have not changed essentially from then until now.) The disappearance of the coral reefs in the higher latitudes during Late Mesozoic then denotes the commencement of the general cooling of the polar regions which eventually led to the glaciations and to the formation of the marked hydroclimatic zones.

The temperatures in the abyssal deep-sea during the Early Tertiary, on the basis of these considerations, were assumed (e.g. by Murray 1895 p. 1456) to have been markedly higher than now, probably about 10°C. Apparently a final proof of this assumption was the palaeotemperatures estimated by Emiliani & Edwards (1953) and Emiliani (1954) by the method of oxygen isotopic analysis on bottom foraminifera from deep-sea cores from depths of about 4000 m in the eastern tropical Pacific, viz. about 10.4°C in Middle Oligocene, 7°C in Lower Miocene, and 2.2°C in uppermost Pliocene; while the bottom temperature in the region in Recent is a little less than 2°C.

Recently, however, Birstein (1959) and Zenkevitch & Birstein (1960 p. 13) noted that the palaeotemperatures determined may not refer to the abyssal but to the bathyal and sublittoral zones, since the foraminifera (in the Middle Oligocene sample, *Cassidulina spinifera,* and in the Lower Middle Miocene sample, *Gyroidina zelandica* and *Laticarinina bullbrooki*) might have been shelf species, of which the empty shells were secondarily shifted to a greater depth.

It is true that for this reason the quoted palaeotemperatures do not offer the ultimate proof of a higher temperature in Early Tertiary. On the other hand the assumption of a higher abyssal temperature at that time appears well-founded alone from the presence of coral reef faunas in the higher latitudes. The foraminifera in question may well also have lived in the abyssal depths as originally assumed. (A recent species of *Gyroidina, G. soldanii,* is recorded as having a bathymetrical range of about 40 to 4350 m, being abundant at the greater depth, which will indicate that this was also its habitat, and a recent species of *Laticarinina, L. pauperata,* is recorded as having a range of about 300 to 3980 m, being abundant e.g. at a depth of 1650 m (Cushman 1931).)

Zenkevitch & Birstein apparently assume that the abyssal temperatures have been continuously low far back in the history of the oceans. At least they (p. 13) consider Bruun (1956) to be in error when he infers that "the relatively sudden onset of the glacial age and its cooling of oceanic deep water must have been catastrophic for the abyssal and hadal faunas", and "only the relatively eurythermic and eurybathic species could survive". They also note (p. 13) that another fact disproving the probability of sharp temperature changes in abyssal waters, is the undoubtedly long existence of several ancient species in these waters, e.g. *Neopilina.* As shall be discussed in a following paragraph (cf. p. 191) it is by no means certain, however, that *Neopilina* has lived continuously in the abyssal deep-sea from Cambro-Silurian times.

(A decrease in abyssal temperatures of a magnitude of 8°C since the Middle Oligocene, about 35 million years ago, means a yearly decrease of an average of $0.23 \cdot 10^{-6}$°C only; and therefore the assumed extinction of the greater part of the possibly earlier existing Palaeozoic and Early Mesozoic abyssal fauna will have been a gradually proceeding phenomenon during the whole of the Tertiary period rather than a relatively sudden mass-mortality at the initiation of the glacial epoch).

The reasons for the undoubtedly well established general climatic change in the later geological history of the earth are obscure, but must be correlated with a change in cloud amounts, precipitation, forces of wind, and oceanic currents; perhaps ultimately depending on a change in the solar radiation. A possible shifting of the position of the poles may also have played a role.

The amount of water in the oceans has most probably been about the same since Early Palaeozoic as it is to-day, and it is probable also that the chemical composition of the oceans has been fairly stable throughout the fossil record (see e.g. PEARSE & GUNTER 1957 p.133). – In the recent deep-sea, the salinity is on an average 34.8‰, and varies only about ± 0.2‰.

A more detailed review of the life conditions in the deep-sea would not be appropriate here. Reference is given to e.g. the summaries presented by EKMAN (1953*a*), FAGE (1953), and BRUUN (1957). The possible influence exerted on the distribution of the benthic fauna by the various ecological features in the deep-sea will be discussed in more detail, however, in chapters XII-XIV.

X. THE THEORETICAL COMPOSITION OF THE DEEP-SEA FAUNA

The first life in the sea must have evolved in the lighted regions, and a floating or swimming life may have existed all over the oceans in the upper waters while a higher bottom life was still restricted to the shallow coastal waters (life in the dark deep-sea not being possible until a source of food was created by organic matters produced in the lighted regions sinking to the depths). Bacterians, able to live under possible anaerobic conditions, must have been the first kind of life in the deep-sea. Occasional wanderers from the upper pelagic fauna must have continually strayed into the dark deeper waters, and eventually it has become possible for pelagic scavengers and predators to live there permanently. Ultimately then, the higher bottom fauna spread outwards from the coastal regions, descending further and further out onto the ocean floor. The exact kind of animals first to settle in the deep-sea, and when this ocurred, is a question which will always remain unanswered. It would seem, however, that some reasonable theories on the origin of the recent abyssal deep-sea fauna can be deduced.

Theoretically the recent deep-sea fauna (since an ocean with great depths must have existed since Praecambrian times), could be composed by elements of Palaeozoic and Mesozoic geological age as well as those of a Caenozoic age. These elements could either have originated in the shallow waters and thereafter merely have extended their range to the depths, or they could, after having become deep-sea dwellers, have been so strongly modified that they can now be regarded as having evolved (as taxons of higher rank than genera), within the deep-sea itself.

The following brief discussion will center on three main categories of faunistic elements in the abyssal region:

1) The possible Palaeozoic element, which should comprise animal types which, almost unchanged during the course of their evolution, have lived in the sea since Palaeozoic times, without having been influenced by variations in such ecological factors as depths and temperatures.

2) The Mesozoic and Early Caenozoic elements, which will include animal types which have not been modified to any marked degree after having extended their range to the deep-sea, as well as such types which by radical modifying of older (Palaeozoic or Mesozoic) deep-sea forms have evolved into forms which are now endemic in the deep-sea. (If their shallow-water relatives have become extinct, the forms of the former category will be relicts in the deep-sea, but they will appear endemic if the shallow-water forms in question have left no fossil record).

3) The Late Caenozoic elements, in which the taxons of family or higher rank will all be immigrants simply because the time lapse within the period is presumably too short for more than the evolution of genera or species. – The time of the immigration into the abyssal region, and also to some extent the place of origin, may be discussed on a firmer basis regarding this category than is possible with regard to the geologically older categories.

XI. THE GEOLOGICAL AGE OF THE RECENT DEEP-SEA FAUNA

1. The alleged antiquity

(Including a discussion of the view held by ZENKEVITCH & BIRSTEIN 1960)

Early in the history of the deep-sea exploration it was generally expected that the great depths would prove to be inhabited by a fauna corresponding to that known from Early Tertiary deposits, an expectation inspired by the finds of various forms related to or reminiscent of forms known previously as fossils from the Tertiary and Cretaceous periods. (The most celebrated of these is the minute sea-lily *Rhizocrinus lofotensis* which was described by M. SARS in 1864; others include various echinoids and molluscs.)

However, the assumption of the deep-sea fauna being essentially archaic became untenable from the results of the Challenger investigations. It is true that WYVILLE THOMSON in 1877 (p. 353) stated, "the abyssal fauna is certainly more nearly related than the fauna of the shallower water to the fauna of the tertiary and secondary periods, although this relation is not so close as we were first inclined to expect". It must be borne in mind, however, that what WYVILLE THOMSON understood by the "abyssal fauna" was the entire deep-sea fauna, including that of the more moderate depths (the bathyal fauna) which harbours, as is to be discussed in the following, a larger percentage of ancient forms than that of the greater depths. Furthermore, the rarity and novelty of the deep-sea forms led them to be erroneously endowed with too great an importance as indicators of antiquity, in comparison with the commonly occurrent and familiar littoral forms such as *Lingula* and *Limulus*.

The first clear denial of the concept of the true deep-sea fauna being an archaic relict fauna, was given in 1880 by MOSELEY who pointed out (p. 571) that: "Contrary to anticipation, the deep-sea fauna is mainly composed of more or less modern shallow-water genera and their allies. The fish of the deep-sea comprise amongst them no Dipnoi, no Ganoids, and no Lampreys ... There are no Trilobites in the deep-sea, and no Graptolites, no Bellemnites. All the most ancient forms which now survive occur in shallow water. Lingula, most ancient of all, is abundant in two or three feet of water ... Trigonia and Limulus survive in shallow water, and so do Amphioxus and Cestracion ..." MOSELEY further pointed out: "scarcely a single animal ... of first-rate zoological importance was obtained in great depths", which, he emphasized, "is a most extraordinary fact, for in our deep-sea dredgings we have explored for the first time nearly three-quarters of the earth's surface".

Yet the fauna of the deep-sea, despite its not being fundamentally different from that of the shallow-water, was revealed by the Challenger Expedition to comprise a number of peculiar families and also higher taxonomic categories. The most sensational perhaps was the discovery (WILLEMOES-SUHM 1873) of the occurrence in the deep-sea of decapod crustaceans belonging to a group, the Eryonidea, which was known from Jurassic deposits, but considered extinct since that time. (A recent representative of the same group was described in 1862 by HELLER, but no mention of its fossil relationships was then made).

The Challenger Expedition was also responsible for showing the importance in the deep-sea fauna of the group of holothurians now known as the order of Elasipoda. This expedition also brought to light the first representatives of the Porcellanasteridae, the only family in the suborder Cribellosa within the Asteroidea. It was left to the Galathea Expedition, however, to collect (at a depth of 3570 m off the Mexican west coast) the first abyssal animal of really "first-rate zoological importance", viz. the mollusc *Neopilina,* described by LEMCHE in 1957 and found to be a living representative of the order Tryblidiacea in the class Monoplacophora, a group dating back to Cambrian and hitherto supposed to have become extinct already fairly early in Palaeozoic (Late Devonian).

The colloquium On the Distribution and Origin of the Deep-Sea Bottom Fauna held in 1953, led to conclusions (cf. SPÄRCK 1953) closely agreeing with those drawn by MOSELEY (op. cit.), viz. that the deep-sea fauna could not be considered to be of any special age, that it certainly included some few archaic (i.e. Mesozoic) forms, but in the main was composed of representatives of shallow-water groups which penetrate into the great depths, and that such a penetration is still in process.

An attempt to give a numerical expression of the relative geological age of the recent marine fauna in various zones of depth, was made by MENZIES & IMBRIE in 1958. They surveyed a number of invertebrate groups where sufficient information was available and found the generic composition of the fauna to be as follows: 1) in depths exceeding 3000 m (the abyssal fauna), about 86 % Tertiary, 14 % Mesozoic, and no Palaeozoic types, 2) in depths between 200 and 2000 m (the bathyal fauna), 62 % Tertiary, 37 % Mesozoic, and 1 % Palaeozoic types, 3) in the intertidal depths, 66 % Tertiary, 30 % Mesozoic, and 4 % Palaeozoic types. Molluscs were not among the groups considered, but *Neopilina* was noted as the only Palaeozoic relict known in the abyssal fauna. (As shall be touched upon in the following, also some other invertebrates of Palaeozoic relationships occur in the abyssal deep-sea, but none of these are peculiar to the region).

The benthic foraminifera were found by MENZIES & IMBRIE to show a higher percentage of genera extending from Palaeozoic to Recent than any of the surveyed invertebrate groups, and also the highest abyssal Palaeozoic generic representation. Since, however, cases of convergency may be more difficult to detect in the foraminifera than in the invertebrates, foraminiferan phylogenetical taxonomy may be less reliable. All the same it seems most likely that foraminifera were rather the earlier colonizers of the deep-sea than was higher life, and also better survived the changes in deep-sea temperatures since Palaeozoic. When A. AGASSIZ (1888 p. 157) supported the opinion that the first benthic invertebrate inhabitants of the deep-sea dated back no further than the Cretaceous, he also noted: "Of course, there must have been pelagic animals, and foraminiferans may have lived at great depths in the track of the currents."

Russian scientists, working with the rich material collected during the recent Russian deep-sea explorations, seem to have adopted the assumption that the deep-sea fauna on the whole has a general antiquity. It is not a Palaeozoic but a Mesozoic origin which they attribute to the abyssal fauna however, and this is also usually understood as being the whole fauna below a depth of about 600 m. Thus ZENKEVITCH in 1959 lists a number of echinoid families, "well known from Upper Cretaceous deposits and formerly thought to be extinct", as being ancient inhabitants of the abyssal zone (i.e. the depths below 600 m).

All the same, the differently expressed opinions of the age of the deep-sea fauna, by, on the one side ZENKEVITCH & BIRSTEIN and on the other e.g. BRUUN (1956) and MENZIES & IMBRIE (op. cit.), does not merely rest on the different use of terminology but has a background too in somewhat different interpretations of the facts known. ZENKEVITCH & BIRSTEIN (1960 p. 10) state that "the percentage of primitive archaic forms in the abyssal fauna is far higher than in the fauna of the shelf, thus providing evidence of the greater antiquity of the abyssal fauna". They note further (p. 14) that the groups discussed by MENZIES & IMBRIE include only 11 % of all species encountered below 3000 m, and that the extent of the conclusions drawn by these authors (viz. the concept of a relatively young abyssal fauna) to the whole abyssal fauna "is unlikely to be correct when they are based on so small a fraction".

It is true that since adequate palaeontological data are lacking with regard to a considerable part of the deep-sea fauna, MENZIES & IMBRIE were unable to discuss its palaeontological relationships in great detail. But the results they arrived at are closely parallel with the general impression of the age/-depth distribution of the marine fauna which MOSELEY held (cf. above). As will be discussed in the following, also various other considerations can but lead one to the assumption that in the main the recent abyssal deep-sea fauna is of no great age, and that at least, the concept of it being essentially archaic is erroneous.

ZENKEVITCH & BIRSTEIN (p. 16) claim that "when we determine the geological age of the genera and families which today live at a given depth we are certainly not determining their actual age, but are merely establishing to which shallow-water fauna of particular periods they are related". The writer fails to understand, however, why this should not be a fairly reliable estimate of the (maximal) geological age of the deep-sea forms.

In theory, a taxon of e.g. family rank could have evolved in the abyssal deep-sea, and thereafter extended its range of distribution upwards, in competition with the bathyal and sublittoral faunas. But this course of events, if ever having taken place at all, will be the exception and the reverse the rule. ZENKEVITCH & BIRSTEIN also note (p. 12) that in their opinion "no formation of major taxonomic units occurred under abyssal conditions: there was simply an adaptive radiation into species and genera".

This view is also held by the writer (on the condition that 'abyssal' is taken in the restricted sense, meaning depths exceeding about 2000 m, and that allowance is made for possible exceptions with regard to taxons of family rank, among which e.g. the actiniarian group, the Galatheanthemidae, may be a case). In the writer's opinion the quoted view will certainly mean, however, that the geological age ascertained through fossil evidence on former shallow-water relatives of any one recent abyssal deep-sea group (if the fossil record is not too incomplete) will at the same time be the maximal age of the group in the abyssal deep-sea.

ZENKEVITCH & BIRSTEIN further state (p. 16) that "The earlier the migration (into the deep-sea) the less likely that the affinity can be traced between a recent deep-water group and a shallow-water group of the past ...", and that the assumption "concerning the higher proportion of ancient elements in the fauna of the shelf as compared with the abyssal depths can be easily explained by the obvious fact that it is not the fauna of the abyssal waters but the fauna of the shelf that has been preserved in fossil condition".

(The taxons of higher rank which are more or less exclusively confined to the recent deep-sea are few. There are e.g. within the molluscs, the Monoplacophora (cf. below), within the crustacea, the Neotanaidae and the Eryonidea (cf. p. 194), and within the echinoderms, the Porcellanasteridae and the Elasipoda).

Zenkevitch & Birstein (1960 p. 12) now consider that "those higher taxonomic units, mainly, or entirely confined to great oceanic depths, should be most correctly regarded as relicts which in former times lived under the favourable conditions of the shallow seas and were displaced by relatively young and more progressive groups". The writer is unable to agree completely with this conclusion however (see also p. 197).

Thus, the two characteristic deep-sea groups among the echinoderms, the Porcellanasteridae and the Elasipoda, which Zenkevitch & Birstein list as ancient relicts in the deep-sea, are in the writer's opinion, examples of higher taxons which have evolved in the upper deep-sea, in the region of the mud-line (cf. p. 200) at the end of the Mesozoic era, and first extended their range to the abyssal zone during Tertiary. The Porcellanasteridae are regarded (cf. chapter VI) not as archaic, but rather as paedomorphic paxillose phanerozoniate sea-stars of a comparatively young phylogenetical origin (cf. pp. 184, 194); and a similar point of view may be adopted for the Elasipoda (cf. p. 194). Both groups are without fossil records.

Peculiarly enough, Zenkevitch & Birstein (p. 12) when giving their opinion on the taxonomic groups confined to the deep-sea conclude: "Whether their descent into great depths and disappearance from shallow waters occurred during the Palaeozoic, Mesozoic, or Cenozoic, is a matter of secondary importance". This question in the writer's opinion is on the contrary a very important one, although in general difficult, if not impossible to answer.

Take e.g. *Neopilina* (inclusive of *Vema*), the only Palaeozoic relict so far recorded from the abyssal fauna. This mollusc, known in Recent solely from depths between 3000 and 6000 m in the eastern tropical Pacific, belongs to a group, the Tryblidiacea, known from Cambro-Silurian deposits, but without fossil records since that time. The group may have been already represented in the abyssal deep-sea in the Early Palaeozoic, but it is also conceivable that, when during Devonian times it disappeared from the fossil record, it was still confined to moderate depths, and not until a much later geological period extended its range also to the abyssal zone. – If it was at all possible, it would certainly be of great interest to ascertain during exactly which geological period the form became abyssal.

If the invasion of the abyssal deep-sea by the ancestors of its recent fauna has taken place almost exclusively since Mesozoic (and many considerations lead to this conclusion), then the abyssal fauna must be considered relatively young (in comparison with the bathyal and the littoral warm-water fauna), no matter which types of animals are now dominant in the region.

Zenkevitch & Birstein (p. 12) conclude: "We can, however, be sure that the great oceanic depths play the part of refuges for relatively primitive relict groups which in their struggle for existence had to desert the more favourable conditions of life in the shallow waters." As already stated the writer considers this point of view unwarranted. Those groups which during evolution became adapted to the life on a soft bottom, such as the Porcellanasteridae and the Elasipoda, and are now abundantly represented, by species and individuals, in the abyssal deep-sea, are conquerors of this habitat rather than refugees into it.

When discussing the young elements in the deep-sea fauna, Zenkevitch & Birstein (p. 20) refer to a characteristic difference in the pattern of vertical distribution between these "secondary deep-water forms" and what they consider "the ancient deep-water forms": "In most secondary deep-water animals the number of species regularly and rapidly decreases with increasing depth, whereas in the ancient deep-sea animals the number of species tend to increase with depth and begin to diminish only with the passage to the lower abyssal and the ultra-abyssal waters". In the writer's opinion this fact is correlated not merely with possibly a different geological age, but equally as much with the fact that the "ancient deep-water forms" are those forms especially adapted for a deep-sea life, being pronouncedly soft-bottom dwellers. (They have evolved in the region of the mud-line (see p. 200) and have spread from there over the deep-sea bottom and into the greater depths with similar ecological conditions, but were prevented in spreading upwards into the shallower water on account of the greater competition from other animals there (cf. p. 200) and the more unstable ecological conditions).

2. The Mesozoic and Early Caenozoic elements

The following review of some of the characteristic abyssal animal forms together with information of their known geological age (according to Müller 1957-60, Treatise of Invertebrate Paleontology 1953-

59, and Traité de Paléontologie 1952-53) will show that a late Mesozoic origin (i.e. a continuous history in the deep-sea since that time) is in general the earliest possibility indicated. There do occur in the abyssal region, it is true, various animal types which show a Palaeozoic relationship, belonging as they do to orders which are known from the Palaeozoic. The families in question, however, cannot usually be traced further back than the Mesozoic. It should be borne in mind too that the immigration of the various groups into the abyssal deep-sea may well have taken place late in their geological history (see also p. 191).

The abyssal poriferans belong to orders which date back to Cambrian. The Hexactinellida e.g. constitutes a very characteristic element in the recent deep-sea fauna; and members of this group, which flourished already in Devonian, are often quoted as examples of a survival of Palaeozoic types in the deep-sea. None of the families to which the recent genera belong, are, however, known from further back than Cretaceous.

The order of Scleractinia (= Madreporaria) is known from Triassic, and the characteristic solitary deep-sea corals belong to suborders which are known from Late Jurassic. The oldest known recent genera, *Deltocyathus* and *Stephanocyathus* (syn. *Stephanotrochus*), date from Eocene.

The order of Octocorallia is mainly represented in the deep-sea by groups without fossil records. The Primnoellidae, which comprises the deepest occurring species of gorgonarians, is known from Cretaceous. The genus *Primnoella,* to which the few abyssal species belong, has its main distribution in shallow water however, and moreover, the abyssal forms are dwarfed (MADSEN 1956*a*). It may he ustifiable therefore to consider the invasion of the deep-sea habitat a late event in the history of the family.

The subphylum the Pycnogonida is known from late Devonian, but the order of Pantopoda, to which the abyssal families belong, is without fossil record.

The subphylum Crustacea, which is one of the dominant groups in the abyssal depths, dates back to Cambrian, and e.g. the order of Decapoda, to which the Eryonidea referred to above belong, is known from Devonian. The Eryonidea themselves are known from Upper Jurassic and seem to have become extinct in the shallow depths during Cretaceous, at least they are without fossil records since that time. Thus this group is a Mesozoic relict in the deep-sea (i.e. the bathyal zone, cf. pp. 194, 197). Two other groups of decapods with representatives in the abyssal region, the Galatheidae and the Homolodromidae, are known from as far back as the Jurassic.

In the Brachiopoda the two cosmopolitan abyssal species (cf. p. 206) belong to orders dating back to Ordovician and Devonian. The genera, however, are known only from Recent.

The Bivalvia are represented in the abyssal region by species of e.g. the families Nuculidae and Ledidae of the taxodonte order Nuculacea, which is known already from Silurian. These bivalves are abundant, however, in the Arctic sublittoral and also in shallow water in temperate regions. Therefore, the extension of their distribution to the deep-sea may well be a comparatively late geological event. The Cuspidaridae of the heterodonte order Poromyacea, is another group of bivalves with several abyssal representatives. It is known from Triassic and is also represented in the sublittoral of colder regions.

In the phylum Mollusca belongs further the only really archaic form known from the abyssal zone, viz. *Neopilina* (inclusive of *Vema*) of the order Tryblidiacea and class Monoplacophora (cf. p. 189).

The stalked crinoids constitute a very characteristic element in the deep-sea, and are often considered the indication of an ancient origin of its fauna. The recent forms are thus generally referred to as the last and feeble survivors of a once flourishing type of animal. Stalked crinoids existed already in Ordovician, and an abundance of species are known from all later periods. However, all the Palaeozoic orders seem to have become extinct during Late Palaeozoic and Early Mesozoic, and the single recent order, the Articulata, can be traced back only to Triassic.

The majority of the recent stalked crinoids, and e.g. all the larger forms, are primarily bathyal in their distribution, thus requiring temperatures higher than 4°C. The family Hyocrinidae, which is known from Quaternary, comprises 5 recent genera. It has a bathymetrical range of between 700 and 4640 m, with the least specialized (and thus oldest) genus, *Calamochrinus,* confined to the depths between 700 and 1400 m (GISLÉN 1953).

The stalked crinoids which occur in the abyssal depths are all small and dwarfed in comparison with the bathyal forms. Stalked crinoids do not now occur in really shallow water, where, however, unstalked free-living forms also of the order of Articulata, are abundant.

Crinoids are probably on the whole as common in the recent oceans as ever they were in the ancient ones, and in some areas this also applies to the stalked type. Some very large recent stalked species form veritable forests in depths of a little more than a hundred meters in both the West Indian and East Indian regions, and other species occur in vast numbers in other areas. Prior to the Challenger Expedition only a few recent specimens were known however, and these could consequently be considered the last rare survivors of a once flourishing group. Although long ago proved untenable, this view on the stalked crinoids is still manifest in handbooks and textbooks. – That the stalked type of crinoid is such an extremely common fossil is explained by its exceptional suitability for fossilation; both on account of its solid calcareous skeleton and by the fact that its habitat is in calm waters where sedimentation may quickly cover its dead remains.

The Echinoidea is another group of echinoderms with characteristic representatives in the deep-sea and with a fairly well-known geological history. The most ancient of the recent groups is the order Cidaroidea, which dates back to Carboniferous. The order comprises (according to MORTENSEN 1928) 10 recent genera with a total of about 80 species, the majority of which live at depths between about 100 and 1000 m. Thirteen species occur between 1000 and 2000 m; while only 4 occur between 2000 and 3000 m and 3 between 3000 and 4000 m. The small number of species of cidaroids occurring in the abyssal region compared to the abundance of species in the upper bathyal and sublittoral depths, may well be an indication that the immigration of the group into the abyssal zone is a rather late event in its geological history. (But of course this conclusion may be objected to on the grounds that the more varied ecological conditions in the moderate depths are more apt to lead to speciation than the stabler ecological conditions in the deep-sea).

The only order of echinoids which descends into the hadal zone, the Spatangoida, is a young type dating back only to Cretaceous.

A few of the examples given in the preceding illustrate how, within the various groups, it is often the youngest forms which have descended furthest down in the deep-sea. It should be noted also that the two abysso-hadal isopod genera, *Eurycope* and *Storthyngura,* often quoted as being examples of primitive types surviving in the great depths, may (as stated by WOLFF in 1959*b*) be in reality the most highly developed types within the asellote crustaceans.

Further, it will appear from this brief survey of some of those characteristic deep-sea animals whose geological history is more or less known, that only a few of the recent abyssal animal forms belong to families which can be traced as far back as the Middle or Late Mesozoic eras. Families of Mesozoic origin play, contrariwise, a fairly important role in the recent bathyal and littoral faunas (cf. p. 189); and those Mesozoic forms which now live in the abyssal region and have bathyal and sublittoral relatives, may well be only Tertiary immigrants in the region. The general absence of definitely archaic animals in the abyssal region may be an indication that the recent abyssal fauna as a whole dates back no further than Late Mesozoic at the earliest. The same age therefore, may be attributed to the endemic abyssal families and orders: a Late Mesozoic origin also being assumed, from another point of view, with regard to the Porcellanasteridae (cf. p. 184).

Within the echinoderms there are besides the Porcellanasteridae (cf. pp. 184, 194) some other groups of higher taxons, characteristic of the bathyal and abyssal depths, which, since they are without known fossil representatives, similarly may be assumed to have evolved within the deep-sea itself (in Late Mesozoic, as discussed above). These are e.g. the asteroid family (or order) the Brisingidae, the echinoid family the Pourtalesiidae, and the holothurioid order the Elasipoda.

Some Middle-Cambrian fossils were, it is true, originally described as elpidiid holothurioids (= Elasipoda), but as discussed by the writer in 1956 and 1957, they were without doubt wrongly interpreted. The supposed occurrence of elasipods in the Middle-Cambrian shallow sea, was otherwise one of the main bases for the assumption by A. H. CLARK in 1913 (in a discussion of the fossil marine faunas in relation to the recent deep-sea fauna) that progressive distance from land in the Palaeozoic sea would be the biological equivalent to progressive increase in depth in the recent deep-sea. (The further from land the less the inorganic material in the water and the fewer the plankton organisms, resulting in less and less favourable biological conditions).

The order of Elasipoda is often, like the Porcellanasteridae, considered to be an archaic group, but, as in the latter group, the apparent archaic character is rather embryonic. The spicules of the Elasipoda frequently resemble developmental stages of spicules in other holothurian orders, and the stone canal opens on the body surface, while in the adult specimens of the other holothurian orders the connection with the surface is usually lost. The writer thus presumes that also the evolution of the Elasipoda was correlated with the phenomenon of paedomorphosis.

The reasons for the smaller percentage of animals of Mesozoic types in the abyssal rather than in the bathyal and littoral regions, and the general absence in the abyssal region of Palaeozoic animal types, may be sought for in the geological history of the oceans and found in changing conditions of environment; the most important being the change in temperatures which have taken place in the deep-sea during the Mesozoic and Caenozoic eras.

The existing deep-sea fauna must have been subjected to a very selective influence when, at the end of the Mesozoic era, the general cooling of the regions of higher latitudes commenced, and when during Late Tertiary and Early Quaternary colder water slowly filled the deeper parts of the ocean basins (cf. p. 187). Those stenothermic types which were adapted to temperatures of about 10° C or more (and were unable to acclimatize themselves to the changing conditions of environment) have accordingly been eliminated in the abyssal region.

This assumption offers a reasonable explanation for the insignificant role played by Palaeozoic types of animals in the recent abyssal fauna, since naturally it might be expected that these older types would be the most affected by the deterioration of climate; presumably being more conservative in their demands on the ecological conditions than the younger types. With the exception of the remarkable case of *Neopilina* it also seems that most of the "living fossils" are now confined to the shallower water of the warmer regions of the sea, where they live at temperatures approximately corresponding to those at which their ancestors may have lived in ancient times. (A possible Early Palaeozoic deep-sea fauna will have been subject to a similar destructive influence by the climatic changes connected with the Permian glaciations).

Forms belonging to a possible older Mesozoic fauna element in the abyssal region may, similarly, have been largely destroyed by the progressive decrease in temperature there during the Tertiary. It would seem that Mesozoic types had a better chance of survival in the bathyal region where the temperatures range up to about 10° C, corresponding to the supposedly almost universal deep-sea temperature in the Late Mesozoic and Early Tertiary periods. Such Mesozoic types of animals, and also of course Palaeozoic ones, which now live in the abyssal region with the very low temperatures (0°-4° C) may very possibly be the descendants of bathyal survivors which did not until Tertiary extend their range downwards, gradually replacing the dying out older abyssal fauna.

The case of the Porcellanasteridae may be quoted as a typical example of this course of events. In all probability this group evolved from astropectinid-like ancestors, which, in Jurassic and Cretaceous times, migrated from the sublittoral region of the Tethys Sea (cf. pp. 184, 200) to the bathyal depths, where the most primitive porcellanasterid genera still occur. From there the Porcellanasteridae then, during Early Tertiary, commenced an invasion into the abyssal region where most of the (from an evolutionary point of view) more advanced genera are now to be found. To judge from the distribution of *Eremicaster* and *Porcellanaster* (cf. p. 212), this invasion into the greatest depths is still going on.

In this connection attention may also be called to the case of the Eryonidea. This order of decapod crustacea, which, as mentioned, dates back to Jurassic, is still represented in Recent by a Jurassic family, the Polychelidae, and includes three other families, the Tetrachelidae, the Coleiidae, and the Eryonidae s. str., known from Triassic-Cretaceous deposits (cf. Balls 1957 p. 1563ff.). The members of the Polychelidae are blind, deposit-feeding forms with feeble mouth parts, whereas the other forms had well developed eyes and stronger mouth parts, and were no doubt predatory. Thus the deep-sea dwelling recent Eryonidea are the direct descendants (cf. also p. 196) of those Late Mesozoic sublittoral-bathyal forms which, as deposit-feeders, were especially suited for a deep-sea life and could persist in the bathyal depths, while their predatory sublittoral relatives were exterminated in their habitat (at the beginning of the Tertiary or earlier).

The Eryonidea comprises two recent genera: *Polycheles* (with 20-30 species) and *Willemoesia* (with half a dozen species). The bathymetrical range is from about 200 m to 4400 m. *Polycheles* is exclusively bathyal, *Willemoesia* abyssal, but only three species are recorded from below 3000 m, and only one from below 4000 m. Thus the Eryonidea are bathyal-upper abyssal in their distribution (they have also pelagic larvae), and while they are of a Late Mesozoic origin in the bathyal zone, their immigration to the abyssal zone may be a much later event in their geological history.

Deep-sea groups of more comprehensive taxonomic categories such as the Porcellanasteridae (= suborder Cribellosa) and the Elasipoda within the echinoderms, and the Neotanaidae within the crustacea are rather few. On the other hand a considerable number of genera, and of course species of diverse other groups, are endemic in the abyssal region. Thus, to judge from the surveys published in the Reports of the Swedish Deep-Sea Expedition and from other surveys compiled by the writer, about half of the species hitherto recorded from depths exceeding 3000 m seem to be exclusively confined to these depths.

3. The Late Caenozoic elements

In the preceding chapters two types of elements in the abyssal fauna were discussed: 1) the possible Palaeozoic element, which was found to be insignificant, and 2) the endemic element of higher taxonomic categories which must be considered geologically to date from Mesozoic, but which at the same time may not have extended their range from the bathyal to the abyssal region until during Tertiary.

There yet remains to be discussed the non-endemic abyssal fauna element of taxons higher than genera. Reference has been made to some of those groups which already in Mesozoic times must have lived in the bathyal region, i.e. the geologically old groups which have an extensive deep-sea distribution (some of them now more or less rare, perhaps even extinct in the sublittoral region), and which probably had begun the immigration into the abyssal region fairly early in Tertiary. Amongst these are the recent Hexactinellida, crinoids (order Articulata), Cidaroidea, and Eryonidea.

Other groups which, since their recent shallow-water relatives live in the tropical sublittoral, may have extended their range to the abyssal region fairly early during Tertiary (before the fall in the abyssal temperature had begun to tell) are e.g. the Gorgonaria, the Astropectinidae, most decapod crustaceans, and the Macrouridae.

(The endemic deep-sea groups, and the other groups of a long-standing occurrence in the deep-sea are often called primary deep-sea forms, while the younger deep-sea groups, with close shallow-water relatives, are called secondary deep-sea forms (see also p. 208)).

A Late Tertiary invasion of the deep-sea may be assumed to have taken place with regard to those groups which are extensively distributed in the abyssal zone, and have their shallow-water relatives in the colder regions. A Late Quaternary (post-glacial) invasion, however, must have taken place regarding those species which have their main distribution in the cold polar shallow-water and from there, being eurybathic, extend into the neighbouring deep-sea with identical temperature conditions. (The latter species, to a considerable extent, may be only guests in the region).

The polar element in the deep-sea fauna is very prominent. Early in the history of the exploration of the deep-sea, when it was discovered that many of the animals inhabiting the North Atlantic depths were identical with forms known previously from the polar shallow water regions, it was accordingly assumed that the deep-sea had been colonized by a mainly Arctic (and Antarctic) fauna (WALLICH 1862, LOVÉN 1863 e.g.).

The recent abyssal fauna includes, on the whole, a very large number of diverse species which have their main distribution in neighbouring bathyal depths, and are either in the course of extending their range permanently to the abyssal zone or are only more or less accidental inhabitants (guests) there (cf. p. 208).

The larger percentage of Tertiary animal types in the abyssal rather than in the bathyal fauna (cf. p. 189) must be an indication, as already noted (see p. 193), that the colonization of the abyssal depths by their recent fauna has been a markedly later event than the colonization of the bathyal zone. On the whole it would seem that the larger the depth the younger the inhabitants, from a geological point of view. Documentation in support of this assumption is given e.g. in the bathymetrical distribution of the various genera of Porcellanasteridae (cf. p. 184). Attention may also be called to the fact that while the liparid fishes, a group without special adaptations for a deep-sea life and with many representatives in shallower water of colder regions, are found down to depths of more than 7500 m, the endemic families of oceanic deep-sea fishes, with light and tactile organs, have hitherto only been found down to depths of about 5500 m (cf. RASS 1959).

The relation between the recent abyssal fauna and the polar shallow-water faunas which are subjected to similar conditions of temperature, should be discussed in more detail.

In the high latitudes in Late Mesozoic times, when the deterioration of climate began and the Jurassic coral reefs and their associated faunas disappeared, the relatively few eurythermic species which survived, and the already cold-adapted ones from the highest latitudes (cf. below), could increase their number of individuals considerably, in accordance with the general rule (perceived by Möbius as early as 1877) that the biomass which may be supported in a given habitat will be present, irrespective of the ratio between species and individuals.

The fauna elements which due to the lowered temperatures became extinct in the high latitudes evidently were (as was similarly assumed to be the case in the deep-sea) the oldest, i.e. most of the Palaeozoic and a major part of the Mesozoic types. At least none of the so-called "living fossils" such as *Lingula* and the others listed p. 189 occur in the higher latitudes.

The gradual cooling during Tertiary must have set in initially in the higher latitudes where the water must always have been somewhat cooler than in the rest of the ocean. The first relatively cold-adapted forms must have evolved here and those which were eurybathic were then able to spread to the deep-sea along with the gradual lowering of temperatures there, and replace those older forms which eventually became extinct. Examples of such Tertiary invaders of the deep-sea may possibly be the bivalve groups Nuculacea and Poromyacea (Cuspidaridae) and among fish, the Liparidae. Mostly however, it is not higher taxons but only genera and species which belong in this category.

Still later, when the extensive glaciations set in, the northern waters became extremely cold. Presumably a number of species were eliminated there for this reason, whereas they survived in deep-sea regions with suitable temperatures. Although it is difficult to give definite examples, any species or genus peculiar to the oceanic deep-sea and belonging to families with a wide distribution in the shallower waters of the temperate regions, could belong in this category.

The Antarctic region has had fairly stable climatic conditions throughout the Caenozoic and far back in the Tertiary period when the cold climate developed (cf. Priestley & Wright 1928). The benthic shallow-water (sublittoral and upper bathyal) fauna here is also richer in species and genera than that of the Arctic, and, as suggested by Wyville Thomson (1877), a fair portion of the bathyal deep-sea fauna may have been derived from the Antarctic fauna.

It may be noted that just as polar species may extend into the deep-sea, the reverse can also occur, and truly deep-sea species reach up into comparatively shallow water in the higher latitudes when temperature and other conditions permit (cf. p. 200). Wyville Thomson (1873 p. 44) mentioned this possibility, and Moseley (1880 p. 546) considered it an established fact. The distribution of the deep-sea holothurian *Elpidia glacialis* is a fine example of the phenomenon.

As soon as the first accurate knowledge of the oceanic deep-sea fauna was obtained, it was recognized that this fauna must have derived from that of the shallower water by continuous downwards and seawards migrations of diverse animal forms. Thus Murray (1895 p. 1436) noted that the relatively large number of genera in the deep-sea in proportion to the number of species "could be accounted for by such migrations having taken place at many different periods of time and from many different parts of the world" and (p. 1454) "There are many indications that the migration into the deep-sea has taken place continuously since Mesozoic times, and is even now going on".

As discussed in the preceding pages, it is possible in some cases to estimate roughly the geological period when the colonizing of the deep-sea by certain groups of animals took place. In some few cases it may even be possible to establish the time of immigration fairly exactly also for those immigrations which took place before the time of the Caenozoic glaciations.

Thus, by correlating the fossil records of some groups of recent deep-sea crustaceans with the palaeographic character of the ocean, i.e. whether in a period of transgression or regression, Beurlen (1931) considered it possible to establish the time of their invasion into the deep-sea. Beurlen refers 1) to the Eryonidea (cf. pp. 192, 194), known as fossils from Late Jurassic, a period of transgression, until Early Cretaceous, when a regression set in, and to the Homolodromidae which, he states, behave in a similar way; 2) to the Dynomenidae and Homolidae, known as fossils from Middle Cretaceous, a period of transgression, and according to him, disappearing from the fossil record in Late Cretaceous when a regression began; 3) to the Geryonidae and Carcinoplacidae, known as fossils from Early Tertiary, a period of transgression, but, again according to him, disappearing as fossils with the beginning of the transgression in Oligocene.

Beurlen now concludes that the immigration into the deep-sea by the groups in question has taken place simultaneously with their disappearance from the fossil record. During the periods of transgression, the extension of the shallow sea (the shelf sea) is greatly enlarged, with the result that many diverse groups flourish. When regression sets in and the area of the shelf sea gradually becomes diminished, the result is a greatly increased competition between the various groups: to some of them this means, considers BEURLEN, the choice between extinction or escape into a new and different habitat.

On three occasions since Jurassic, notes BEURLEN, an immigration of decapod crustaceans into the deep-sea took place. Further, he points out that together with these three invasions into the deep-sea, a fourth is now in progress, induced by the regression during Diluvium and Recent, and exemplified by the bathymetrical distribution of the Maiidae and Leucosiidae.

BEURLEN's reflections on the immigration into the deep-sea by these crustacean groups are most interesting. Nevertheless, his conclusions that: it is only under compulsion of actual geographical developments that the animals penetrate into the inhospitable deep-sea region, in order to take refuge, may not be the correct presentation of the course of events.

Those groups of deep-sea animals which were formerly represented in the shallow depths but which are now extinct there, are, it is true, commonly described (cf. p. 191) as having withdrawn to and taken refuge in the deep-sea after having been forced away from the ecologically more unstable shallow-water regions by more vigorous competitors. It is hardly feasible, however, that an animal group on the verge of extinction in one habitat, would be able to extend its range to a new one with different ecological conditions. The conquering of a new habitat undoubtedly requires vigorous and adaptable immigrants. (A different phenomenon altogether is the spreading to another zone of depth along with an extension or displacement of water-masses offering suitable ecological conditions, e.g. accounting for the submergence of shallow-water polar animals into the deep-sea).

With regard to the fossil records of the decapod groups examined by BEURLEN, these must be most complete from periods of transgression, since most known fossil marine faunas naturally date from such periods. Furthermore, animals which are mostly bathyal in their distribution are usually poorly represented as fossils from periods later than Cretaceous and Early Tertiary (as fossil marine faunas known since this time are, on the whole, from sublittoral or littoral habitats). A comparison with the surveys given by BALLS (1957) shows that BEURLEN's presentation of the facts is also somewhat simplified, since some of the discussed families actually have a more continuous fossil record than he acknowledges. Thus, the Dynomenidae and Homolidae are known from about the middle of Tertiary, and the Geryonidae from late in Tertiary. Further, the groups discussed are mostly bathyal in their distribution in Recent. The Carcinoplacidae are, besides being represented in bathyal depths, abundant in the littoral region, and the Dynomenidae are actually only sublittoral.

The initial invasion of the deep-sea, i.e. the bathyal region, by the decapod families mentioned, very probably took place while they were most widespread and abundant and thus actively evolving in the shallower depths. Then, after having become successfully adapted for a deep-sea life they may gradually have extended their range to still greater depths (cf. p. 200), while their shallow-water relatives possibly became extinct as a result of changed ecological conditions in their original habitat.

Of the groups considered by BEURLEN only the Eryonidea (represented in Recent by the family the Polychelidae) reach into really abyssal depths, i.e. depths of more than 3000 m (cf. p. 194).

XII. THE FACTORS DECIDING THE VERTICAL ZONATION OF THE DEEP-SEA FAUNA

Apart from food and oxygen being necessary for the existence of a higher marine life, the most important single factor for controlling the distribution of the animals in the marine habitat is unquestionably the temperature. This was more or less clearly realized by the first biogeographers; as was also observed early on (e.g. by WYVILLE THOMSON 1873) that the extremes of temperature, rather than the means, is the regulating factor.

The known bathymetrical distribution of the Porcellanasteridae constitutes a further support of the, on the whole, well established assumption that in the oceanic deep-sea the upwards limit of the true abyssal fauna (i. e. the boundary between this and the bathyal fauna) is primarily determined by the course of the 4° C isotherm (or at least coincides with it). Thus, all six abyssal genera (listed p. 180) are known solely from localities with temperatures below about 4° C.

The highest temperature endured by the Porcellanasteridae as a whole, seems to be between 11° and 12° C. One of the three bathyal genera (listed p. 180) is known from localities with temperatures varying from 1.1° to 11.3° C, while the two others, known from only a few finds, lived at temperatures ranging between 6° or 8° and 11.5° C. The absence of the Porcellanasteridae from the abyssal depths in the Mediterranean (where the bottom temperatures are above 13° C) is well in agreement with an upper limit for the tolerances of temperature at about 12° C.

In the warmer regions of the ocean, an important distributional barrier is set (as regards the pelagic fauna) by the so-called thermocline, or discontinuity layer (the water layer where the warmer surface water, sinking downwards due to the evaporation causing increased salinity – and thus increased density – meets and mixes with the underlying colder water of an equal density). The whole water-mass, the hydrosphere, is by this water layer subdivided into a warmer upper water-mass and a colder lower water-mass (called by Bruun (1955*b*) thermosphere and psychrosphere, in order "to stress this salient ecological factor"). In the upper warm low-density water-mass (varying in thickness between 20 and 500 m or more) the temperature decreases rapidly from somwhat below the surface and downwards. In the thermocline (varying in thickness from a few to more than a hundred meters) it falls gradually, generally from about 15° to 10° C; while below the thermocline it decreases only very slowly towards the bottom.

The pelagic order of deep-sea fishes the Ceratoidea (i. e. the adults) is pointed out by Bruun as an example of an animal group with a distribution confined to the psychrosphere: (being represented in the Sulu Sea, where the bottom temperatures are about 10° C, but absent from the Mediterranean deep-sea, where the bottom temperatures exceed 12-13° C (cf. Bertelsen 1951)).

The Porcellanasteridae may now be quoted as an example of a benthic group which similarly has its distribution within the psychrosphere.

Since in the oceanic abyssal region the temperature is almost uniform at all depths, most authors, including e. g. Moseley (1880 p. 545), have considered it improbable that the fauna there would exhibit any distributional depth zones, or at least, no distinct ones. However, now that more and more abyssal species have been found in wide-spread localities, perhaps even in different oceans, it seems that several of them may actually be confined to rather narrow zones of depth. Thus, within the Porcellanasteridae all fifteen finds of the cosmopolitan *Styracaster horridus* were made between 4040 and 5610 m, and all seven finds of the cosmopolitan *Eremicaster vicinus* between 5200 and about 7200 m.

That the abyssal region s. str. in faunistic respect is to be subdivided into an upper and a lower zone is a conclusion that has been arrived at by various authors working on different groups of invertebrates and fish (and was indirectly suggested in Murray's survey (1895) of the number of species occurring in different zones of depth). When surveying the vertical distribution of more than a thousand species of bottom invertebrates from below 2000 m, N. G. Vinogradova (1958) found that generally this change in the composition of the species occurs at about 4500 m (varying in different groups from 4000 to 5000 m).

The bathymetrical distribution of the Porcellanasteridae shows the following boundaries: 1) an upper limit for the group as a whole (and for the bathyal genera in particular) at a depth of about 1000 m, and a temperature of about 12° C, and 2) an upper limit for the abyssal genera at a depth of about 2500/3000 m, and a temperature of about 4° C. The latter boundary is at the same time the lower limit for the bathyal genera. Further, there is a change in the composition of the species at about 4000/5000 m (supporting the distinction at this depth between an upper and a lower abyssal zone). The greatest depth at which porcellanasterids have been collected is about 7600 m, which is somewhat down in the hadal zone.

The extreme depths of the oceans (the trenches) are now, as mentioned, distinguished as a separate faunistic region, the hadal zone, since, besides several species, a number of genera and even two families (the benthic actiniarians the Galatheanthemidae and the pelagic amphipods the Vitjazianidae) appear to be endemic there. – Moseley (1880 p. 546) also pointed out: "Were there any variations in the conditions of life such as to restrict certain animals to very great depths, as mountain plants are restricted to certain heights on land, then we might expect to find a peculiar fauna in the deep depressions, and especially in the deepest hollows on the bottom of the sea, where the water is over 4.000 fathoms deep." He concluded, however, that such conditions would not be present. – The upper limit of the hadal region was originally set at about 6000 m, but, according to WOLFF 1960, is better set at 6800/7000 m.

Within the Porcellanasteridae only the cosmopolitan *Eremicaster vicinus* was hitherto recorded from the hadal zone, but having a known bathymetrical range of 5200 to 7200 m it may not be a truly hadal species. (As mentioned p. 181 also *Porcellanaster* has now been found in hadal depths, at about 7600 m).

A possible earlier Palaeozoic element in the hadal fauna has been subjected to the same destructive influence through the progressively lowered temperatures during the Tertiary as has a such element in the abyssal fauna. It is unlikely, therefore, that the hadal fauna should include any elements of more ancient origin than those found in the abyssal fauna. The adiabatic rise in temperature in the depths of the trenches is so small ($\leqq 0.2°C$) that one has to dismiss the possibility of a stenothermic species surviving there when the further cooling exterminated it in the abyssal depth.

The trenches are usually considered to have a late geological origin; it being assumed that they were formed in connection with the Alpine foldings, i. e. in Late Pliocene, near the end of the Tertiary period (cf. e. g. UMBGROVE 1947 p. 63). This being so the hadal fauna must be relatively young. However, certain authors, e. g. BIRSTEIN (1959), are of the opinion that the hadal fauna, as known at present, repudiates such a late formation of the trenches (see also p. 212).

The evolution of taxons of higher than specific rank, such as genera and families, must be put back at least into the Tertiary period. Therefore, as discussed in the preceding, such groups which are now endemic in the deep-sea, must have existed there prior to the beginning of the Quaternary period, long before the last glaciations.* It is quite conceivable, however, that those animal groups which seem to be endemic in the hadal depths, have invaded these depths during the Quaternary from the lower abyssal zone. That they have not yet been found there is, of course, no definite proof of their absence.

The hadal fauna, as is the case of the abyssal fauna, also includes a considerable number of forms of a decidedly young origin. WOLFF (1956*a* p. 152) e. g. came to the conclusion that the hadal isopods had derived from cold areas in the Arctic, and especially in the Antarctic regions. This is an indication that the trenches, at least in part, did not become inhabited with their present fauna until after the cooling at the poles had reached its climax, and stenothermic cold-adapted species had developed in the waters there (cf. p. 196).

Evidently the temperature, although it is an extremely important factor, does not solely determine the vertical distribution of the Porcellanasteridae (or any other group in the deep-sea), considering the very slight differences in the temperatures of the upper abyssal, lower abyssal, and hadal zones. When seeking for another factor to explain these zones of distribution, one might turn to that of pressure. What actual significance this factor may have for the deep-sea animals is rather unknown however; all experiments on the effects of pressure on marine animals having of necessity been made on shallow-water species. (Some of these, incidentally, have shown a surprising resistance to increased pressure, even surviving short exposures to pressures of 1000 atm. (cf. CATTELL 1936 p. 441)).

The boundary between the upper and lower abyssal zones, at about 4500 m, almost coincides with the depth at which the water becomes undersaturated with calcite (cf. REVELLE & FAIRBRIDGE 1957 p. 282). Thus, this and other chemical properties of the water (modified by increased pressure) may be partly the explanation for the faunal change.

That the pressure, however, is a less important factor for the distribution of the deep-sea fauna than the temperature, is borne out also by the findings of ZOBELL & MORITA (1959) that the deep-sea bacteria, which "were unique in their ability to grow preferentially or exclusively at in situ hydrostatic pressures" at the same time "appear to be even more heat-sensitive than pressure-sensitive".

The percentage of species of porcellanasterids in the total fauna of sea-stars varies, as illustrated in the diagram p. 180, from 0 in the depths less than about 1000 m, to 25 % at 4000 m, 50 % at 6000 m and (so far known) 100 % at 7000 m. The apparent absence of the Porcellanasteridae in more moderate depths, even in the polar regions where some other deep-sea animals may occur in fairly shallow water (cf. p. 196), might lead to the assumption that these sea-stars are dependent on a hydrostatic pressure of a definite size. However, the explanation for the upper limit of their occurrence is more likely to be found in their relations to other animals in the habitat, competitors for food and predators.

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* This seems evident and has also been concluded by most if not all authors since the days of the Challenger Expedition. BIRSTEIN (1959*b* p. 228) is incorrect in attributing to BRUUN the view that the abyssal fauna should be "of a recent (Quaternary) origin, derived from batial and sublittoral species". What BRUUN (1956) said in effect was that the glacial cooling of oceanic deep water "must have been catastrophic for the abyssal and hadal fauna" so far as "Only the relatively eurythermic and eurybathic species could survive".

Thus, the probable low reproductive rate in the Porcellanasteridae (cf. p. 181) may limit their ability to compete with other deposit-feeding animals in more moderate depths, such as e. g. bivalves. When the Porcellanasteridae are more successful in the greater depths the reason may be that they are better able to thrive on a bottom relatively poor in food than most of their potential competitors. This latter possibility may account too for the apparently fairly uniform distribution of the Porcellanasteridae over the whole abyssal plain (cf. p. 214).

Further, a low reproductive rate will make the populations of Porcellanasteridae very susceptible to attacks from predators. It is possible therefore, that the upper limit of their occurrence is also set as the depth at which the depletion by predators outweighs the ıeproductive potential. – That in the deep-sea fauna the percentage of carnivores relative to suspension-feeders and deposit-feeders decreases with increasing depth, is a well-known phenomenon (cf. e. g. IMBRIE 1959), and is also illustrated in the diagram referred to above, showing the percentage occurrence of species of the mud-eating porcellanasterids in various zones of depth relative to the total number of species of sea-stars; these animals in general being the most important benthic carnivores.

Other factors which may influence the upwards vertical distribution of deep-sea fauna elements, (in areas where no limit is set by the temperature) are e. g. the water movements (the mud-dwelling deep-sea fauna requires a soft bottom and calm water) and possibly the light. When many deep-sea animals extend their range of occurrence high up in the polar waters, this, as already suggested by MOSELEY (1880 p. 547), may be due not only to the low temperatures but also to the fact that the water here "is dark during most of the year, both from the absence of sun or the obliquity of its rays, and because of the covering of the water by ice and snow".

The boundaries in the vertical distribution of the marine fauna are naturally never sharply defined but are transitional zones. The lower limit for the vertical distribution of a deep-sea species once having become adapted to the abyssal conditions of temperature, is probably always determined by a combination of factors, including perhaps the chemical properties of the water, conditioned e. g. on the pressure, and the correlated condition of the bottom substrates (see p. 213ff). Further, a most important factor must always be the question of food-supply.

XIII. SOME CHARACTERISTICS OF DEEP-SEA ANIMALS

Any fundamental differences between the fauna of the deep-sea and that of the shallow water were not to be expected, since ultimately the former is derived from the latter, and since the environmental conditions in the deep-sea, apart from the pressure, are no different from any that can be found in shallow regions. The characteristic features shown by many deep-sea animals are also primarily correlated with their life in a dark and calm milieu and on a soft bottom.

The affinity of the (known) deep-sea fauna with the soft bottom environment was stressed by MURRAY (1895 p. 1434) when he introduced the term "mud-line" for the depths (at about 50-500 m) where the detrital matters with organic particles derived from land and from the death and decay of pelagic organisms, begin to settle on the sea-floor. "Here," he noted, "is situated the great feeding grounds of the ocean". MURRAY further assumed that this region of fine mud was for many species the place of origin, and suggested that: "In all probability the deep-sea was peopled by continuous migrations downwards and seawards from about the mud-line."

The case of the Porcellanasteridae can be taken as an example of a deep-sea group which has originated in the region of the mud-line. The astropectinid-like ancestral porcellanasterids (cf. p. 184) may be assumed to have settled in the upper deep-sea in Late Mesozoic times. Thereafter, in the course of their evolution, they have become adapted to living as burrowers in the loose substratum; completely forsaking the predatory or scavenging way of feeding (which was presumably their original habit) for the mud-eating habit, now one of their distinct characteristics. After having succeeded in this new mode of life, the Porcellanasteridae spread outwards and downwards in the deep-sea simply because the life-conditions, to which they were now adjusted, were also found there.

The Porcellanasteridae in morphological respect, are primarily distinguished by their complicated cribriform organs (cf. p. 181), and simple cribriform organs are found in the sublittoral-bathyal Goniopectinidae. On the whole, the peculiarities of the Porcellanasteridae are merely the adaptation to life on a soft bottom and to feeding on the organic material contained in the bottom substratum itself (the ciliated cribriform organs producing a circulation of fresh water around the animal in its burrow, and at the same time providing a flow of surface substratum down to the animal to feed on).

The "mud-eating" habit is a frequent way of feeding in motile benthic deep-sea animals, and is met with in other echinoderm groups such as e. g. the Elasipoda and the Spatangoida, and e. g. in some polychaetes and crustaceans. Even some species of fish, of the family Macrouridae, feed in a rather similar way.

Light-perceptive organs are absent in the Porcellanasteridae (Meurer 1915) whereas they are found in some other deep-sea dwelling asteroids such as e. g. astropectinids. This fact might be taken as further evidence of the long geological time the Porcellanasteridae may have lived exclusively in the dark deep-sea. However, as is known from other animal groups, the eyes are organs which may easily degenerate if not in use.

A characteristic feature in many sessile deep-sea animals (e. g. some glass-sponges, sea-pens, sea-lilies, and some sea-squirts) is that they are provided with a stalk. This in general is claimed to be a necessary adaptation for a safe anchoring and for lifting the animals above the substratum, the upper layer of which is usually assumed to be in a semi-liquid state.

The photographs of the deep-sea bottom now available, usually seem however, to indicate a fairly firm surface. In the opinion of the writer, the stalk of the sessile abyssal animals may also be an adaptation for raising them above the oxygen-poor water layer close to the bottom rather than for raising them above a semi-liquid layer of ooze. Of course the stalk also keeps the sessile animals somewhat free of the ooze clouds which will be stirred up whenever an animal moves over the bottom. However, in this connection it should be borne in mind that such suspended particles will often be their main source of food.

The peculiar structural feature of a chitinous tube formed around the body in the Galatheanthemidae (the possibly endemic hadal sea-anemone discovered by the Galathea Expedition and described by Carlgren (1956)) may be an adaptation analogous to a stalk, since its support allows the oral end with the tentacles to be raised well above the bottom.

In the abyssal tunicate *Culeolus,* the thread-like stalk probably cannot lift the body off the bottom, but serves in keeping it at anchor while, as suggested by Millar (1959), it floats by means of periodic unstimulated contractions and the expelling of water, such as has been observed in some shallow-water tunicates. A favourite place of attachment for *Culeolus* is also the stalk of glass-sponges, no doubt because in this way it becomes further raised above the bottom.

The problem of a possible gigantism in the deep-sea has been brought forward by various authors. Thus the Challenger scientists, e. g. Moseley (1880 p. 593), noted that "Some animal forms appear to be dwarfed by deep-sea conditions of life", while "Others attain under them gigantic proportions".

Pronounced examples of dwarfing are found in the deep-sea species of such sessile suspension-feeders as the gorgonarian *Primnoella* and the stalked crinoid *Bathycrinus,* and in these cases the dwarfing seems to be well accounted for by the sparse food-supply available to this kind of animal. But not all sessile suspension-feeders in the deep-sea are small. There are actually giant forms too; the most remarkable example being the gigantic solitary hydroid *Branchiocerianthus (Monocaulus* of authors) of which the Challenger (cf. Wyville Thomson 1875) dredged specimens more than 2 m high, in the mid-Pacific and near Japan at about 5200 and 3500 m respectively. It perhaps may be justified to assume that such large specimens are of great age.

Several abyssal crustaceans show so-called gigantism and e. g. Birstein (1957) and Wolff (1960), when referring to this feature, have suggested that it might be due to an especially high metabolic rate, effected by the hydrostatic pressure in the great depths, – experiments having shown that intensified pressure causes an increase in the rate of metabolism. The increased metabolic rate in an animal reacting to such adverse conditions as that of a pressure a hundred times greater than the habitual one is, however, quite another thing than the rate of metabolism in an animal living undisturbed in its natural milieu. As regards that very important ecological factor the temperature, the prevailing rule also seems to be that different populations of the same or related species show roughly the same metabolic rate, regardless of the temperatures at which they live (cf. Bullock 1955). No doubt the rate of metabolism in populations of the same or related species will prove to be similarly adapted to the pressure at various depths.

Cases of 'gigantism' may occur in quite different ecological milieus. Marine invertebrate species (and genera) primarily show relatively increased size in the cold regions (the polar seas and the deep-sea), whereas terrestrial species (and genera) primarily show this feature in the warm regions of the tropical rain-forests. However, the giant-clams are examples of 'gigantism' in the tropical shallow-sea, while the giant-earthworms are examples of 'gigantism' in only a moderately warm terrestrial milieu.

Thus, in the writer's opinion, it seems most probable that the phenomenon of gigantism in the deep-sea, as understood by e. g. Birstein and Wolff (op. cit.), does not really exist. (Dwarfing, or relatively reduced size, induced by the extremely unfavourable conditions in the deep-sea with regard to accessibility of food, is, on the other hand, a well-established phenomenon).

The increased size encountered in some deep-sea forms was suggested by Moseley to depend "on lack of enemies rather than on an abundance of food". The progressively fewer predatory species in the benthic fauna with increasing depth and distance from land must also be a factor which allows the abyssal animals a relatively long life in general. – Furthermore, the sparse food-supply may cause a relatively slow growth in the abyssal animals and accordingly, a postponed sexual maturity in comparison with that of their relatives from shallower depths. At the same time the abyssal animals may perhaps attain a great longevity simply on account of the uniform ecological and homothermal conditions in the deep-sea. It is also suggested, by e. g. MacGinitie 1949, that some deep-sea animals have life spans of perhaps hundreds of years. If this be so, it may well explain some cases of so-called gigantism.

As regards the Porcellanasteridae, none of the species are especially remarkable in their size. The smallest, *Porcellanaster cæruleus,* reaches a diameter of about 6 cm, and the largest, *Styracaster horridus,* reaches a diameter of 30 cm (but has very slender arms). The total range of size in sea-stars goes from a few centimeters to about three quarters of a meter in diameter, and by far the greater part are from 10 to 30 cm in diameter.

The assumption of entirely uniform ecological conditions in the deep-sea habitat throughout the year will not be true everywhere. The marked seasonal fluctuations in the productivity in the upper layers of the oceans in some areas may be perceptible in the deep-sea too. Moseley (1880 p. 592) also noted: "Possibly there is at some places a periodical variation in the supply of food falling from above, which may give rise to a little annual excitement amongst the inhabitants."

This could mean, for the abyssal fauna, a seasonally fixed sexual period (or spawning time). No evidence is available to support the possibility however. It is also commonly assumed that the abyssal species as a rule will not show any definite seasonal period of reproduction but may spawn at any time of the year. What very little can be deduced from the examination of the gonads of a number of porcellanasterids agrees with the assumption that eggs in small numbers may be produced throughout the whole year. A non-pelagic development is considered the general rule for all truly abyssal species, and according to their egg-sizes the Porcellanasteridae also follow this rule.

In the oceanic abyssal region with its rather stable ecological conditions (without considering the gradual change in temperature during an entire geological era), the incentive for new forms to evolve will probably be insignificant. At least, this is the general assumption. The many species and genera, and also higher taxons, which are endemic in the region, are in the main therefore, only the results of those genetic changes which occur in all populations in the course of time (cf. p. 204).

XIV. THE HORIZONTAL DISTRIBUTION OF THE ABYSSAL FAUNA

1. The cosmopolitanism

The first naturalists who investigated the distribution of marine animals (e. g. Woodward 1851) early observed that the deeper a species (or a genus) lives, the more extensive generally is its horizontal distribution (i. e. towards the higher latitudes, correlated with the downwards decreased temperature). The earlier authors who discussed the deep-sea fauna consequently anticipated that it should prove to be cosmopolitan. Thus Lovén in 1863 distinctly expressed the opinion that a deep-sea fauna of the same general character extended from pole to pole, including some very widely distributed species. Wyville Thomson in 1877 similarly concluded that the depths of more than 1000 m all over the world had a uniform fauna, that the abyssal genera were generally cosmopolitan, and the species were the same, or, if differing in remote localities, then markedly representative, i. e. of close genetic origin. The uniform impression given by the abyssal fauna is also amusingly expressed in Moseley's remark (1880 p. 547): "We got quite tired on the Challenger of dredging up the same monotonous animals wherever we went."

That the deep-sea fauna should prove to be essentially cosmopolitan, not only as regards the genera, but also to a large extent with regard to the species, was in effect the classical view, based on the assumption that the conditions of environment were identical all over the ocean. (That the zoogeography of the shallow and moderate depths is primarily a question of the distribution of different water masses with which the different species are associated, was more or less clearly realized by the first biogeographers and also alluded to by Wyville Thomson in 1873 p. 42).

The view of a general cosmopolitanism of the abyssal species has been opposed however, by later investigators. Murray, when summarizing the Challenger results, thus had to conclude (1895 p. 1439) "with references to species there is no striking evidence of a universal deep-sea fauna spread all over the floor of the ocean". Most recently e. g. N. G. Vinogradova (1959) has expressed the opinion that the deep-sea bottom fauna should be divided into a series of separate zoogeographical regions. This point of view will be discussed in more detail in a following paragraph (cf. p. 209).

It has been amply proved in the course of the exploration of the deep-sea that the fauna of the more moderate depths, the bathyal fauna, has to be distinguished into a number of different zoogeographical divisions. Their extension and the causes for them does not, however, concern us in the present discussion, which is limited to the truly abyssal fauna.

Within the Porcellanasteridae, nearly all the abyssal genera are known to be cosmopolitan, viz. *Hyphalaster* (2275-5415 m), *Thoracaster* (2600-about 5000 m), *Styracaster* (2550-5610 m), *Eremicaster* (1570-about 7200 m), and *Porcellanaster* (1160-6035 m), while the bathyal genera seem to have a restricted distribution, none of them being known from outside the Indo-Malayan region, viz. *Lysaster* (about 1000 m), *Benthogenia* (905-925 m), and *Sidonaster* (1150-about 2300 m). The remaining abyssal genus, *Abyssaster* (3200-6280 m), is known only from the Indian Ocean and the western Pacific. (A new abyssal genus, *Vitjazaster,* from the Kurile-Kamchatka Trench, will be described by Belyaev).

A cosmopolitan distribution is undoubtedly the general rule for all truly abyssal genera; the exceptions are few, especially considering how scanty the exploration of the deep-sea still is. A reminder of the possible incompleteness of the faunistic record is e. g. the case of the peculiar tunicate *Octacnemus* which was believed endemic in the South Pacific deep-sea from the days of the Challenger Expedition until 1947 when a specimen was recorded among some unidentified North Atlantic material from the Ingolf Expedition (Madsen 1947). One may also mention the case of the Pogonophora, which were considered endemic in the Pacific for some time after their discovery (cf. Bruun 1956), but are now known to be world-ranging.

It may be appropriate, before proceeding with the discussion of the horizontal distribution of the abyssal species, to stress that these are understood to be the species which, always living at temperatures below about 4° C, have their main occurrence in the depths below about 2000 m, and down to 6-7000 m (i. e. to the transition to the hadal zone in which other rules of distribution may be in force, as discussed p. 212).

Every zoogeographical analysis must consider the possibility of erroneous specific determinations. In deep-sea zoogeography however, cases of synonyms among the described species are no doubt more frequent than cases of new species being erroneously identified with earlier described ones. Further, some taxonomists have been so impressed by their knowledge of the zoogeographical regions in different latitudes on land that they have erected new species or subspecies in deep-sea animals for no other reason than that they were collected in localities widely separated from where the related, and, in their morphological characters, indistinguishable forms were known. (Examples of such cases in the history of the Porcellanasteridae are the species *Porcellanaster eremicus* and the subspecies *Styracaster chuni groenlandica)*.

Since the abyssal fauna is still only scantily explored, more importance should certainly be given to similarities ascertained in various areas than to apparent differences, which may be due to e. g. accidental information of rare species or of temporary local faunas (see also p. 214).

The writer in 1951*a*, 1951*b*, and 1953*a*, made some surveys of the distribution of the species recorded from depths exceeding 3000 m in some of the classes of echinoderms. (The limit at 3000 m should warrant that the greater part of the not truly abyssal species were excluded). It appeared from these surveys that about 5 % of the species of asteroids in question and about 10 % of the ophiuroids and holothurioids were known to be cosmopolitan, a fair percentage considering the number of species recorded from only a single or a few finds.

A cosmopolitan species, it should perhaps be noted, is here (in agreement with the most usual view) understood to be a species recorded from the main deep-sea basin of each of the three oceans (typically absent from the enclosed basins with bottom temperatures of more than 4° C, and also, in general, from the Arctic deep-sea region where the temperatures are below 0° C).

Within the Porcellanasteridae the following species, according to the quoted definition, may be considered cosmopolitan: *Hyphalaster inermis* (32 finds, 2280-5415 m), *Thoracaster cylindratus* (20 finds, 2600-5000 m), *Styracaster horridus* (15 finds, 4040-5610 m), *Styracaster chuni* (6 finds, 2550-4550 m), *Eremicaster vicinus* (7 finds, 5200-about 7200 m), and *Porcellanaster cæruleus* (86 finds, 1160-6035 m). That is, six species out of the total of fourteen species known from more than two finds, or an ascertained cosmopolitanism of 43 %.

The species thus considered cosmopolitan may have their center of distribution in a defined area however, and at the greatest distance from this area may occur only sparsely and be very scattered. *Porcellanaster cæruleus* e.g. is known from many finds in the Atlantic and the Indian Ocean, but from only a few finds in the well-explored East Pacific. *Styracaster horridus* and *S. chuni,* besides *Hyphalaster inermis,* also seem to be mainly Atlanto-Indian in their distribution, none of them having hitherto been found in the eastern Pacific.

That the truly abyssal benthic fauna should prove to be essentially cosmopolitan should hardly instigate any serious objections, since the abyssal region forms an ecological unit without pronounced barriers (i. e. disregarding the abyssal depths of such enclosed basins as the Arctic Sea with very low and the Mediterranean with unusually high temperatures).

A similar extensive speciation such as that on land is a priori not to be expected. A new abyssal form when spreading over the deep-sea floor from its center of origin, may in different populations change in different directions however; just as different populations of an "old" cosmopolitan species may develop new distinct characters. This accounts (since the genes responsible for such modifications will not always immediately become spread throughout the whole stock) for WYVILLE THOMSON's observation (1877 p. 353) that deep-sea forms from remote localities often appear markedly representative. (A good example is provided by the two minute deep-sea forms of the gorgonarian *Primnoella* from opposite regions of the globe: *Primnoella jungerseni* from the North Atlantic (2137-2448 m) and *P. krampi* from the South Pacific (5850 m), described by the writer (1944, 1956*a*). These two forms are clearly distinct, but had they been found in the same area there should have been little objection in considering them individual variants of the same species).

It is usually held (cf. e. g. DAHL 1953) that benthic deep-sea forms with a free-swimming larval phase have generally a wider distribution than those without. However, the absence of a free-swimming larval stage does not prevent an abyssal species in eventually attaining a world-wide distribution. This is evident also from the known cosmopolitan distribution of several of the porcellanasterids, the larvae of which are certainly non-pelagic. (The eggs of course may float along the bottom, as may also the larvae a short time before settling). Any abyssal form, wherever it has first appeared as a separate taxonomic unit, will eventually be able to spread over the whole abyssal region.

The abyssal deep-sea is essentially a very calm milieu, but not absolutely so, and certainly not to the degree assumed by the early biogeographers, and illustrated e. g. in MOSELEY's remark (1880 p. 543) that: "Any movement taking place in the water at that depth must be of a molecular nature only." There are in most places bottom currents of some velocity, on an average of 2 km per day (cf. DIETRICH 1957). The currents in abyssal depths (2000-4000 m) in the North Atlantic are e. g. recorded showing a range of velocity variation of 0-5 cm/sek (i. e. up to 4.3 km per day), and a change of direction through at least 90°, over periods of a few weeks and over distances of a few tens of kilometres (SWALLOW & HAMON 1959). Furthermore, earthquakes and volcanic activity may cause stronger currents of a temporary nature which may be of importance as regards the distribution of the animals. – The dispersal of a benthic species from its place of origin and over the whole world ocean, if it e.g. propagates once every year and the offspring settle at a distance of, say, 1 km from the parental populations, might take place in the course of 20-30.000 years (about the time which has elapsed since the last glaciations).

2. Some cosmopolitan species

The taxonomic revision of the Porcellanasteridae undertaken on the basis of the Galathea material, has demonstrated (cf. p. 204) that a considerable number of the species belonging to this group may be termed cosmopolitan (at least they are known to be widely distributed in the oceanic deep-sea). – There are as yet only few taxonomical surveys of deep-sea animals based on sufficiently representative materials for a zoogeographical purpose. But those available (see following summaries) seem strongly to support the assumption that the cosmopolitan pattern of distribution is the general rule as regards the truly abyssal species, i.e. those which are endemic in the region.

One of the more conspicuous animal forms in the deep-sea is the sea-pen *Umbellula.* (During the Galathea Expedition it was collected in 21 of the 74 successful dredgings in depths below 1000 m.) The taxonomy of the genus was revised in 1958 by BROCH, who recognized only 7 distinct species (or 6 species and 1 subspecies) among the total of 39 species which had been named in the literature. (A single name, *Crinillum geniculatum,* refers only to a stalk fragment, and a few nominal species, *U.gilberti, U.indica,* and *U.purpurea,* were not definitely referred to any of the valid species. *U.indica* and *U.purpurea* are probably identical with *U.pellucida* however.)

The following gives the pattern of distribution shown by the recognized species of *Umbellula:*

Two species, *U.lindahli* (150-5310 m) and *U.thomsoni* (about 200-5860 m), are cosmopolitan, (*U.thomsoni* was collected by the Galathea Expedition in the Panamic region). Two other species, *U.huxleyi* (about 300-1365 m) and *U.durissima* (about 570-4450 m), are also recorded from all three oceans, but in the Pacific area only from the regions of the Malay and Japanese archipelagos, and they thus primarily show an Atlanto-Indian distribution.

Two species, *U.pellucida* (220-2000 m) and *U.spicata* (375-1100 m), are known solely from the northern Indian Ocean, and are both confined to the bathyal zone.

The remaining form, *U.encrinus* (180-1500 m), is of an Arctic distribution, and may well be considered an Arctic race of the oceanic deep-sea species *U.lindahli.*

Of the other deep-sea pennatularians, four further species may be termed cosmopolitan (KÜKENTHAL & BROCH 1911), viz. *Anthoptilum grandiflorum* (230-2920 m), *Funiculina quadrangularis* (65-2600 m) (unknown from the East Pacific however), *Distichoptilum gracile* (1190-2830 m), and *Scleroptilum grandiflorum* (820-4200 m).

The solitary madreporarian coral, *Fungiacyathus* (or *Bathyactis) symmetrica* (150-5300 m), is also cosmopolitan (MOSELEY 1880).

Stephanoscyphus simplex, the only scyphozoan polyp known from depths exceeding 3000 m, was dealt with in detail by KRAMP in 1959 on the basis of the Galathea material. It has a world-wide distribution in the oceanic deep-sea (42 finds) in depths from 430 to 7000 m and at temperatures of 0°C to about 10°C (13°C?), its main occurrence being in depths of more than 2000 m and at temperatures below 4°C.

Only a very few bryozoans are known from more than a single find (SILÉN 1951), but one of these, *Levinsenella magna* (1690-4850 m), is known to be cosmopolitan.

The polychaetes on the whole are to a large extent cosmopolitan. KIRKEGAARD (1956) e.g. recognizes in the hadal fauna, besides a special element of stenobathic and stenothermic species, two other elements: "Eurybathic and eurythermic species, many of them, maybe all, cosmopolitan" and "Eurybathic and stenothermic species with a world-wide distribution".

A total of about 45 species of ascidians are recorded from depths of more than 2000 m (Millar 1959); and of those known from more finds, half are cosmopolitan, viz. *Culeolus murrayi* (3400-4635 m), *Dicarpa simplex* (2470-4600 m), *Corynascidia suhmi* (2475-4635 m), *Styela sericata* (3510-5860 m), and *Bathystyeloides enderbyanus* (2550-5300 m).

The majority of abyssal pycnogonids are known from single finds only. But one of the 9 species of *Nymphon, N. procerum* (3950-4600 m), and four of the 12 species of *Colossendeis,* viz. *C. cucurbita* (1350-4400 m), *C. angusta* (12-5350 m), *C. colossea* (865-4150 m), and *C. macerrima* (538-3670 m), are known to be cosmopolitan (cf. Fage 1951).

The cirripeds include 34 species recorded from depths exceeding 3000 m (Nilsson-Cantell 1955), and the only two known from sufficient finds to be used in a zoogeographical analysis, are both cosmopolitan, viz. *Megalasma hamatum* (365-3660 m), and *Verruca gibbosa* (385-3130 m).

Cosmopolitan species are e.g. among the abyssal isopods: *Storthyngura pulchra* and *Eurycope nodifrons* (cf. Wolff 1956), and among the abyssal amphipods: *Orchomenella abyssorum* and *Halice secunda* (cf. Dahl 1959).

The decapod crustacea include a number of cosmopolitan deep-sea species (Balls 1957) such as *Nematocarcinus ensifer* (535-3650 m), *Polycheles sculptus* (450-2870 m), *Galacantha rostrata* (1600-2900 m), and *Ethusina abyssicola* (1225-4260 m). A number of other species are known to be very widely distributed.

Two of the abyssal species of brachiopods are cosmopolitan (Dall 1920), viz. *Pelagodiscus atlanticus* (1500-5000 m) and *Abyssothyris wyvillei* (1800-5500 m).

Two of the 10 species of gephyreans known from depths of more than 3000 m (E. Wesenberg-Lund 1955) are of a world-wide distribution, viz. *Golfingia flagriferum* and *G. margaritacea.*

Among the echinoderms, e.g. 11 of the species of ophiuroids recorded from depths of more than 3000 m, (about one-fifth of the species known from more than one find) are known to be cosmopolitan (cf. Madsen 1951 *b*). As mentioned p. 204, also a fair percentage of the deep-sea asteroids and holothurioids are of a similar wide distribution; and a preliminary study of the echinoids collected by the Galathea Expedition has revealed that e.g. also *Echinosigra phiale* is cosmopolitan (Madsen 1951 *a*, 1953 *a, b*).

Taking into account the few abyssal dredgings which have been performed in relation to the vast distribution of the abyssal region, it is certainly very noteworthy how many abyssal species have been rediscovered in remote localitites. This strongly supports the classical assumption of a uniform abyssal bottom fauna, or, more correctly (cf. p. 207 ff.), of an abyssal bottom fauna in which a large element is the same all over the oceans. It also seems that we now have a fair knowledge of the common forms in this endemic abyssal fauna element, in spite of the somewhat random collecting. Thus the Galathea Expedition obtained porcellanasterids in 27 dredgings spread along its whole circumnavigation route, and not a single one of the species found, was new to science.

The importance which is to be given to the discoveries of the same species in remote localities, will be borne out by the following calculation of how large a part of the abyssal region is hitherto explored. The abyssal deep-sea (with depths exceeding 3000 m) occupies an area of 278 million square kilometers, or slightly more than half the total area of our globe, and the area covered by the dredging operations up to now can at the very most have been 5 km^2. The information we have of the bottom fauna of the abyssal deep-sea thus covers only one-fifty millionths ($2 \cdot 10^{-5}$ ‰) of the total area occupied by this fauna.

3. Ekman's considerations on a possible cosmopolitanism of the abyssal fauna

In his important handbook of the zoogeography of the sea, Ekman (1953 p. 291) states: "The abyssal species have generally a wider distribution than the archibenthal and there are many cosmopolitan species. But the dividing line between the more locally restricted species and the more or less cosmopolitan species with regard to depth should be put at a lower level than the commonly assumed upper limit of the abyssal zone". At the same time he notes: "Not even for the most extreme abyssal species of the benthos can a cosmopolitan distribution, however, be considered the rule.

As will have been evident from the preceding discussion of the horizontal distribution of the truly abyssal species, the writer must disagree with this latter conclusion (which disregards the fact that the majority of the abyssal species are yet known from only a single or a couple of finds). Of course not all animals living in the abyssal region are cosmopolitan. However, if in the analysis of the zoogeography of the abyssal deep-sea, the element of eurybathic species also occurring in the bathyal zone (perhaps even in the sublittoral of the colder regions (cf. p. 208)) is excluded, (besides those species known from too few finds to be of any value for a zoogeographical purpose) then the concept of a cosmopolitan distribution of a large percentage of the species appears well documented.

(EKMAN in his handbook used, for practical purposes, the 1000 m line as the limit between the bathyal and abyssal faunas. – The depth which he (as noted above) refers to as the upper limit of the cosmopolitan species, was suggested by KOFOED (1927), in connection with the distribution of the deep-sea fishes, to be roughly at 2600 m. EKMAN further found in a later analysis of the vertical distribution of the elasipod holothurians (1953 *b*) that in this typical abyssal group the greatest faunal change occurs at a depth of 2000 m. This depth roughly coincides with the upper limit of the occurrence of eupelagic sediments, and therefore, concludes EKMAN, this limit is also a zoogeographical boundary.)

4. The main subdivision of the lower abysssal fauna

The writer's view compared with that held by EKMAN.

The writer has suggested (1951, 1953), on the basis of an analysis of the known distribution of the deep-sea asteroids and ophiuroids, that if any zoogeographical subdivision of the endemic lower abyssal benthic fauna should be undertaken, there might be distinguished – besides the large cosmopolitan element: 1) An element with a distribution extending over the Atlantic and the Indian Ocean (and, as was also noted, inclusive of the neighbouring region of the Malay Archipelago). 2) An element with a distribution confined to the Pacific. 3) An Antarctic element.

It may be worth noting that these three claimed main faunistic regions in the abyssal deep-sea roughly coincide with the three major areas of different deep-sea deposits, viz. globigerina ooze (in the Atlantic and Indian oceans), abyssal red clay (in the Pacific), and diatom ooze (in the Antarctic).

As was also touched upon in 1953, the impression of an Atlanto-Indian element versus a Pacific element in the abyssal fauna, might be caused by an artefact of collecting, the species in reality being cosmopolitan but not yet proven. Primarily, this tentative suggestion of an Atlanto-Indian and a Pacific abyssal fauna region respectively, was also given as an objection to the view held by EKMAN (1935, 1953 *a*), of an Atlantic and an Indo-pan-Pacific abyssal subregion respectively.

EKMAN (1953 *a* p. 292) stated that: "one would not go far wrong in maintaining that the abyssal fauna of the medium degrees of latitude may be divided into two main regions, namely into an Atlantic and an Indo-Pacific, the latter reaching east as far as the American coast. The main divide is here not the East Pacific Barrier (cf. p. 212), as in the case of the shelf fauna, as it is apparently navigable for some abyssal species, but it is formed by the two American continents. Thus a difference has developed between the abyssal and shelf fauna in that (as EKMAN underlined) the abyssal fauna cannot be divided into an Atlanto-East-Pacific and an Indo-West-Pacific region, but into an Atlantic and an Indo-pan-Pacific region".

This view was given by EKMAN in very general terms, whereas he otherwise supported the various claimed zoogeographical regions with faunistic surveys. Thus it appears that he primarily wanted to emphasize the marked difference in the abyssal fauna on either side of the American continents (that is, the Atlantic and the East Pacific abyssal faunas respectively) in contrast to the great similarity between the shallow-water fauna on either side of the Isthmus of Panama. – It is only in passing that he referred to an Atlantic and an Indo-Pacific deep-sea region respectively.

At a later stage in the handbook (p. 303) EKMAN noted that "the open-sea abyssal can be divided zoogeographically into only three or four main regions: an Atlantic, Pacific, arctic and perhaps antarctic region". Thus here he took no definite view on the zoogeographical position of the abyssal fauna of the Indian Ocean. In an other paragraph (p. 292) he also pointed out: "How far the abyssal fauna of the Indian Ocean is independent vis-à-vis that of the Pacific may be shown by future investigations". Further he mentioned (p. 292) that: "Several species which are common to the abyssal region of the Indian Ocean and the Atlantic and which were formerly regarded as Atlantic relicts of the Tethys Sea, are now considered as signs of a direct communication between the two abyssal regions south of Africa". – Apparently the conclusion must be that EKMAN's view on the main zoogeographical subdivisions of the oceanic abyssal deep-sea (i.e., the zoogeographical position of the Indian abyssal fauna) does not actually conflict with that held by the writer. (The probable explanations for a closer affinity of the abyssal fauna of the Indian Ocean with that of the Atlantic rather than with that of the East Pacific, are discussed in paragraph 7, p. 210.)

The writer regrets that the known distribution of the Porcellanasteridae is not of great help in settling the question of the zoogeographical position of the abyssal Indian Ocean. Of a total of 14 species which are known from more than two finds, six (listed p. 204) are cosmopolitan. *Styracaster elongatus* (7 finds) is known from the Atlantic and the Indian Ocean. *Styracaster spinosus* (5 finds) is known from the Atlantic, and probably *S. clavipes,* recorded from a single locality in the Indian Ocean, is the same species. *Styracaster armatus* (4 finds), *Abyssaster tara* (8 finds) and *Eremicaster crassus* (5 finds) are known from the Indian Ocean and the Pacific. *Styracaster caroli* (6 finds) is known only from the Indian Ocean. *Eremicaster pacificus* (15 finds) and *E. gracilis* (23 finds) are known only from the Pacific. Of these eight species of porcellanasterids known from only one or two of the oceans, two range from the Atlantic to the Indian Ocean, while three range from the Indian Ocean to the Pacific.

With reference to the theory of a possible subdivision of the abyssal fauna into an Indo-Atlantic and a Pacific element (besides the cosmopolitan element), attention may be called to the fact that with regard to some deep-sea crustacea, Burkenroad in 1936 (Penaeidae) and Dahl in 1953 (Eryonidea) similarly found a pattern of distribution indicating a closer relation between the deep-sea faunas of the Indian and the Atlantic oceans than between those of the Indian and the Pacific oceans.

5. The "guests" in the abyssal region

In the writer's opinion it should be sufficiently established from the faunistic surveys given in the preceding that the abyssal zone contains a characterizing fauna of cosmopolitan species. There is no absolute faunistic homogenity however, not even in the lower abyssal zone, since existing side by side with the endemic abyssal species there are considerable numbers of species which may be described as guests in the region (cf. below). The presence of these species naturally makes it possible to distinguish several subregions in the abyssal deep-sea, although these refer rather to the bathyal zoogeography. When stating that the open-sea abyssal can be divided zoogeographically into two or three main regions only (see further p. 207) Ekman also pointed out (1953 p. 303) that "for the coastal abyssal and especially for the archibenthal we have to postulate a greater number of regions".

The species in the abyssal fauna, here called guests (a name probably used first by Walther, 1893-94 p. 168), sometimes also called secondary deep-sea species, have their main distribution in a confined area of the bathyal zone (in the case of the polar fauna maybe even in the sublittoral zone). The individuals or populations which occur in the neighbouring abyssal depths may be only strayers, able to live but at the same time (probably primarily because of scarcity of food) unable to produce a constant series of generations under the abyssal conditions. Such species in order to maintain their abyssal representation will depend on a continuous invasion from the bathyal depths and thus will really confirm to the concept of a guest. – Other species may be better adapted to an abyssal existence but still only able to mature their reproductive products under food-conditions such as found on the terrigeneous deposits (cf. p. 186) and for this reason are of a restricted distribution in the abyssal zone. (When finally a species has evolved the ability to reproduce, also when living on the eupelagic deposits, its distribution over the whole abyssal bottom will be only a question of time.)

The most common 'guest' occurrences in the abyssal zone are shown by species which are abundant in sublittoral-bathyal depths in the higher latitudes, and from there descend into the neighbouring greater depths (cf. p. 195). Examples of such cases are offered by e.g. the following three ophiuroids: the Antarctic *Ophiosteira senoqui* (110-3109 m), the Arctic-North Atlantic *Ophiocten sericeum* (6-4370 m), and the North Pacific *Ophiura lectoctenia* (123-3239 m), (cf. the map published by the writer, 1953 *b* p. 36, illustrating the principal types of deep-sea distribution within the echinoderms).

Further examples of species occurring in the North Atlantic deep-sea, but apparently having their main distribution in the sublittoral-upper bathyal depths in the Arctic region, are e.g. within the octocorals: *Clavularia arctica* (55-2050 m), *Gersemia rubiformis* (6-3600 m), and *Capnella glomerata* (60-2700 m), (cf. Madsen 1944), and within the amphipods: *Stegocephalus inflatus* (5-2000 m), *Arrhis phyllonix* (5-2465 m), and *Hippomedon holbølli* (15->2200 m), (cf. Stephensen 1925 p. 129, 1931 p. 232, 1935 p. 71).

It seems probable that a number of the taxodonte

Table 2. The zoogeography of the abyssal region

<table>
<tr><th colspan="3">According to VINOGRADOVA (considering the fauna from depths exceeding 2000 m)</th><th colspan="2">According to the writer (considering primarily the endemic abyssal fauna)</th></tr>
<tr><td rowspan="4">ATLANTIC DEEP WATER AREA</td><td>ARCTIC SUB-AREA</td><td></td><td>ARCTIC DEEP-SEA REGION</td><td></td></tr>
<tr><td rowspan="3">ATLANTIC SUB-AREA</td><td>North Atlantic Province</td><td rowspan="5">ATLANTO-INDIAN (+ WEST PACIFIC) DEEP-SEA REGION</td><td rowspan="7">COSMOPOLITAN REGION</td></tr>
<tr><td>West Atlantic Province</td></tr>
<tr><td>East Atlantic Province</td></tr>
<tr><td rowspan="4">PACIFIC-NORTH INDIAN DEEP WATER AREA</td><td>NORTH-INDIAN SUB-AREA</td><td></td></tr>
<tr><td rowspan="3">PACIFIC SUB-AREA</td><td>West Pacific Province</td></tr>
<tr><td>North Pacific Province</td><td rowspan="2">PACIFIC (EAST PACIFIC) DEEP-SEA REGION</td></tr>
<tr><td>East Pacific Province</td></tr>
<tr><td rowspan="3">ANTARTIC DEEP WATER AREA</td><td>ATLANTIC SUB-AREA</td><td></td><td rowspan="3">ANTARTIC DEEP-SEA REGION</td><td></td></tr>
<tr><td rowspan="2">INDIAN-PACIFIC SUB-AREA</td><td>Indian Province</td><td></td></tr>
<tr><td>Pacific Province</td><td></td></tr>
</table>

bivalves recorded from the North Atlantic deep-sea are also merely "guests" from the Arctic shallow region, e.g. *Nucula tenuis* (5-2250 m) and *Portlandia arctica* (5-2400 m). Other bivalves which show the same kind of distribution are e.g. *Modiolaria discors* (0-1800 m), *Pecten groenlandicus* (6-2000 m), and *Saxicava arctica* (0-2000 m), (cf. MADSEN 1949 pp. 106-112).

Finally, a few examples may be given of species of echinoderms which seem to have their main distribution in the bathyal depths of a confined area in the lower latitudes, while occurring as "guests" in the neighbouring abyssal depths, e.g. the ophiuroid *Ophiotreta matura* (240-4160 m) in the Indo-Malayan area, the asteroid *Rosaster alexandri* (150-3550 m) in the Bay of Mexico (cf. MADSEN 1951 *a, b),* and the echinoids *Phormosoma placenta* (170-2340 m) and *Pygmæocidaris prionigera* (660-2860 m) in the Indo-Malayan area, and *Coelopleurus floridianus* (90-2380 m) and *Homolampas fragilis* (550-3550 m) in the western North Atlantic (the West Indian area), (cf. MORTENSEN 1928-51).

6. Commentary on N. G. Vinogradova's view on the abyssal zoogeography

A scheme giving a detailed zoogeographical subdivision of the abyssal deep-sea has recently been published by N. G. VINOGRADOVA. – It is intended to make a few comments on this scheme since it is somewhat at variance with the view of the zoogeography of the abyssal zone held by the writer.

The accompanying table 2 gives a survey of the zoogeographical areas, sub-areas and provinces, claimed in the deep-sea by VINOGRADOVA, comparing them with the regions claimed by the writer. Table 3 gives a survey of the distribution of the cosmopolitan and the more widely distributed porcellanasterids in relation to the sub-areas and provinces of VINOGRADOVA.

It should be noted that while the writer has

Table 3. The distribution of some of the species of Porcellanasteridae; those considered cosmopolitan marked with an asterisk

	North Atlantic	West Atlantic	East Atlantic	North Indian	West Pacific	North Pacific	East Pacific
* *Hyphalaster inermis*		·	·	·		·	·
Abyssaster tara				·		·	
* *Thoracaster cylindratus*			·			·	·
* *Styracaster horridus*			·		·		
* *Styracaster chuni*			·				
Eremicaster gracilis						×	×
Eremicaster crassus				·			·
* *Eremicaster vicinus*			·	·		·	·
* *Porcellanaster cæruleus*					·	·	·

confined his considerations on the abyssal zoogeography to the fauna occurring in depths of more than 3000 m, VINOGRADOVA based her analysis on the fauna recorded from more than 2000 m, which means that a number of species of an extended bathyal rather than an abyssal distribution have been included. It will also be immediately evident from table 3 that such a detailed zoogeographical subdivision as that proposed by VINOGRADOVA in her provinces, is unreasonable in relation to such truly abyssal species as the porcellanasterids. VINOGRADOVA's provinces really relate to the bathyal fauna, and the following discussion will therefore only consider the sub-areas and areas claimed by her.

According to VINOGRADOVA the zoogeographical sub-areas in the abyssal zone are: the Arctic, the Atlantic, the North Indian, the Pacific, the Antarctic Atlantic and the Antarctic Indian-Pacific.

As to the Antarctic deep-sea, the writer agrees with the, on the whole, commonly held opinion (cf. EKMAN 1953 *a* p. 303) that it constitutes a special faunistic region. All three species of porcellanasterids collected in the Antartic Sea, *Hyphalaster scotiae, Styracaster robustus*, and *Abyssaster planus*, may also be especially cold-adapted forms which may be endemic in the region. (They are known only from the type-localities.)

It is similarly agreed that the Arctic deep-sea, which is an enclosed basin, is a separate zoogeographical region. (No porcellanasterids are known so far from this area.)

As regards the Atlantic, North Indian and Pacific sub-areas then, the abyssal faunas of the Atlantic and the Pacific obviously show distinct features. The North Indian abyssal fauna, however, is so closely related with the Pacific on the one side and that of the Atlantic on the other side, that from a zoogeographical point of view the Indian abyssal region can not be ranked equal with the two other regions. This is also generally recognized. To which of the two other oceanic abyssal faunas the Indian abyssal fauna has the nearest connection is, however, a point of dissension.

Thus the main point on which the writer disagrees with VINOGRADOVA in her view on the abyssal zoogeography, is with regard to the zoogeographical position of the truly abyssal fauna of the Indian Ocean. While VINOGRADOVA postulates an Atlantic deep-water area as distinct from a Pacific-North Indian deep-water area (a division agreeing with EKMAN's Atlantic and Indo-pan-Pacific abyssal regions), the writer postulates an Atlanto-Indian region (inclusive of the region of the Malay Archipelago) as distinct from a Pacific region (cf. pp. 207. 208).

VINOGRADOVA found 2.1 % of the more than a thousand analyzed species to be common to the Indian Ocean and the Atlantic, and twice as many common to the Indian Ocean and the Pacific (further, that only 4 % were known to be cosmopolitan). But, as already noted, the surveyed species have included a considerable number which the present writer would not regard as truly abyssal, and a large number have been recorded from only a single or a few localities, and therefore are of little use for any zoogeographical purposes.

7. Possible explanations for an Atlanto-Indian and a Pacific (East Pacific) abyssal fauna element respectively

It is beyond dispute that the bathyal faunas of the northern Indian Ocean and of the neighbouring West Pacific, are very closely related. It is further evident that also the abyssal fauna is largely the same in the Indian Ocean and in the neighbouring region of the Malay Archipelago (also when disregarding the cosmopolitan element and the element of "guests" from the bathyal zone). This fauna is, however, as already mentioned in the preceding, in the writer's opinion more closely related with the abyssal fauna of the Atlantic than with that of the main Pacific, or rather the northern and eastern Pacific. The supposed boundary or, more correctly, the transitional zone between these two claimed main subdivisions of the oceanic abyssal region extends from Southern Japan in a south-eastern direction to east of New Zealand. (The writer thus distinguishes a Pacific abyssal fauna (in the main comprised by VINOGRADOVA'S North Pacific and East Pacific provinces) from the rest of the oceanic abyssal fauna, whereas VINOGRADOVA, and EKMAN, distinguish the Atlantic abyssal fauna from that of the other oceans.)

The marked differences in primarily the bathyal but also in the abyssal faunas of either side of the American continent, have been noted by several authors. For instance in 1953 DAHL says: "In the round-the-world distribution of the abyssal Crustacea the West-Atlantic and the East Pacific probably represent the opposite extremes". – The distribution of the Porcellanasteridae, as known at present, shows exactly the same picture. In the eastern Pacific, *Eremicaster* is abundant, *Abyssaster, Styracaster,* and *Porcellanaster,* are represented but rare, whereas *Hyphalaster* is unknown. In the Atlantic, *Eremicaster* is only known to be represented by a single, abysso-hadal species, while *Porcellanaster, Hyphalaster,* and also *Styracaster,* are common. In the Indian Ocean these four species all are abundant. Of the two remaining abyssal genera, *Abyssaster* is primarily Indian in its distribution and unknown from the Atlantic, while *Thoracaster* seems equally common in all three oceans.

An explanation for the difference between the deep-sea faunas of the eastern Pacific and western Atlantic, may be found in the geological history of the oceans (cf. Arldt 1919-22; Schott 1912, 1935). In former geological periods, i. e. from Palaeozoic until well up in Caenozoic (Late Tertiary), a great ocean belt, including the recent Mediterranean, stretched across the earth, dividing the land masses into a southern and a northern group. This world-ocean was of a somewhat varying extension in different periods, but already from Early Mesozoic the land masses corresponding to the present North and South American continents were merely separated by a shallow (and narrow) stretch of sea (cf. Schuchert 1935); and at the end of the Mesozoic a land-bridge was erected. (During the middle of the Tertiary this land-bridge was broken, but only to permit the interchange of the tropical shallow water faunas of either side of the isthmus; and at the end of the Tertiary it became closed again.) The differences in the recent deep-sea faunas to either side of the American continent is thus well accounted for.

The recent littoral and sublittoral faunas of either side of the Isthmus of Panama, on account of the interoceanic connection during Late Tertiary, are contrariwise closely related and comprise, besides numerous identical genera, many so-called twin species and also several identical species (cf. Ekman 1953 *a* p. 30). In the shallow-water fauna of the tropical belt the greatest contrast is to be found between the fauna of the western American coast and that of the Indo-West-Pacific region, which, far back in the geological history were continuously separated by a broad and very deep ocean (Ekman's East Pacific Barrier).

The claimed close connection between the abyssal fauna of the Atlantic and that of the Indian Ocean (inclusive of the region of the Malay Archipelago), also illustrated in the distribution of the Porcellanasteridae, is similarly accounted for both by the present wide connection between the two regions south of Africa and by the past history of this part of the world-ocean (cf. Arldt 1919-22).

From Late Mesozoic and into Early Tertiary the regions corresponding to the recent Atlantic and Indian Oceans were in wide connection both north and south of the later African continent (whereas during this period the regions corresponding to the recent Indian and Pacific oceans were to a large extent separated by land or by shallow water). It was not until Late Tertiary that the part of the world-ocean stretching across from the Indian to the Atlantic region, (the so-called Tethys Sea) was replaced by the recent conditions, with a separation of the Indian Ocean, the Mediterranean, and the Atlantic.

The Atlantic region suffered a marked deterioration of climate in connection with the glaciations in its northern part, whereas the ecological conditions remained rather stable in the Indian region during the Tertiary as well as the Quaternary period. The bathyal, and in part, relatively primitive porcellanasterids found in the Indian Ocean, may therefore (as noted in the preceding) be regarded as the last survivors or direct descendants of the ancient species of porcellanasterids which inhabited the bathyal depths of the Tethys Sea, and have now perished in the other regions.

(As pointed out by Ekman (1953 *a*), the rather stable ecological conditions prevailing for such a long time in the Indo-Malayan region offer a better explanation of the general faunal richness found here in comparison with the Atlantic and Pacific, than the assumption that the Indian Ocean has been a center of creation.)

It is assumed that in the oceanic abyssal region there are no zoogeographical barriers of such importance that they can definitely prevent any species, (when first adapted to the ecological conditions in the great depths) from eventually spreading over the whole world-wide abyssal region. Since, however, a dispersal over that vast area by species whose young must typically settle near their parents, may take thousands of years, a species originating in the Atlantic would be common to this and the Indian Ocean for a long time before spreading to the Pacific, and vice versa for a species originating in the Pacific.

The very long geological period during which the abyssal regions of the western Atlantic and the eastern Pacific have been separated is a natural explanation of existing differences in their faunas.

Are there also, however, any reasonable explanations for zoogeographical boundaries elsewhere in the abyssal oceanic deep-sea? Certainly the land mass formed by the European-Asian and African continents constitutes a kind of zoogeographical barrier which will take time to circumvent. Some kind of barrier may also be formed between the Indian Ocean and the Pacific by the Australian continent, supplemented to the south by the extremely cold Antarctic water and to the north by the islands of the Malay Archipelago.

Finally, to all appearances, the so-called East Pacific Barrier, referred to above as the most important zoogeographical boundary in the circumtropical shallow-water region, is also a boundary for the abyssal fauna. The abyssal region stretching from the western North Pacific southwards to the east of Polynesia is a poor feeding ground for benthic animals. It is sparsely populated therefore, and apparently even comprises extensive desert-like areas (cf. p. 214). It must be relatively difficult for an abyssal species to spread from either the western or the eastern Pacific through this sterile region where no large populations can be maintained. Evidently the spreading of the abyssal species in the eastern Pacific also takes place primarily in southwards and northwards directions through the food-rich areas near the continents, and the spreading from west to east in the Pacific, or vice versa, may mainly take place in its northernmost region.

Porcellanaster cœruleus and *Eremicaster gracilis* (inclusive of *E. crassus)* may be species which are in the course of spreading over the abyssal deep-sea from the bathyal western North Atlantic and from the bathyal eastern Pacific respectively. They also seem to dominate widely in the abyssal depths of the mentioned regions, and being young and apparently vigorous types of porcellanasterids, they may have been serious competitors to older types of this group which possibly lived there earlier.

(It would seem that the Porcellanasteridae in general may not be very exacting in their demands on the substratum, at least some of the species being able to thrive equally well on a wide variety of bottom (cf. p. 213). This may be one reason accounting for the fact that these animals apparently are less apt to speciation than some other deep-sea animals, e.g. isopods and amphipods. Thus, the distribution of the various species of porcellanasterids must correspond exceptionally well with the main zoogeographical divisions of the abyssal region.)

8. The alleged endemism in the trench faunas

At this point a few remarks may be made on the zoogeographical position of the hadal fauna. Tectonically the trenches and deeps are rather well circumscribed; this feature probably accounting for a certain isolation of their faunas, and a hereby caused speciation. The possibility must also be considered that the hydrostatic pressure in the hadal zone may require special physiological adaptations of its inhabitants, which subsequently might become unable to thrive under other conditions and so be prevented in spreading from the trenches or deeps. However, this is a possibility which the writer does not think feasible.

It is true that a considerable number of the species recorded from more than 6000 m, are unknown from smaller depths, but this could be partly accounted for by incomplete knowledge of their distribution. From Wolff's survey (1960) it also appears that of the hitherto identified 23 hadal species of echinoderms, more than half, viz. 14, are known to have a more or less wide distribution in the abyssal zone too.

The trenches are usually considered to be of a comparatively young geological age; it being assumed that their formation was connected with the Alpine foldings (cf. p. 199). In the writer's opinion the facts known about their faunas do not dismiss such an assumption. – The degree of endemism recorded for the various trench faunas is partly on the subspecies level, and from this it can not be concluded that the trenches are of any great age. Incidentally, it should always be possible to point out minute differences between different populations, especially as long as only small numbers of individuals, or materials which may only comprise siblings, are available. With regard to the trench faunas it may often be difficult to judge therefore the degree of endemism. Very probably many of the hadal subspecies which have been erected, can not hold when more material becomes available and the range of variation better elucidated. (See also pp. 213, 215).

9. The distribution of the abyssal fauna in relation to the condition of the bottom

Evidently the abyssal fauna is to a large extent composed of comparatively few species which occur in a relative abundance of individuals. This is a feature which is shown also by the cold shallow-water faunas and further by the infauna as a whole. In the former case the feature may be traced back to the fact that only relatively few species survived the Tertiary fall in the temperatures. In the latter case the reason is the relatively few ecological niches available (in comparison with the number available for the epifauna). Known samples of the abyssal fauna also primarily represent the infauna, since almost all successful deep-sea collecting has been done on the soft level bottom. (THORSON, 1957 p. 466, estimates that the total number of epifauna species in the sea is at least four times as large as that of infauna species.)

Although the abyssal deep-sea bottom is mainly flat, areas with an uneven, hard and rocky bottom, are apparently of a more common occurrence than was suspected before the introduction of the echo-sounder. The fauna in such places is yet only very fragmentarily known, and though probably rather poor, may include many unknown forms. Also the general assumption that the character of the bottom substratum is entirely uniform over vast areas may not be true in all places. Areas covered with a very loose substratum of fine ooze may thus include seamounts with a coarser grade of bottom, since here the currents may remove the finest deposits.

Incidentally, the old deep-sea expeditions which had to risk their collecting gear at random, were more likely to obtain samples of the abyssal epifauna than modern expeditions, which, guided by their echo-sounders, have as far as possible used their costly gear for dredging only on the level bottom. Why the hadal fauna seems to be rather different from the known abyssal fauna, is perhaps in part due to the fact that the fauna living on the fairly steep slopes which bound the rather narrow trenches, send strayers out on the enclosed flat bottom areas where the collecting has been largely performed.

The Porcellanasteridae are infauna animals which live from the basal food in the milieu (i.e. eating the bottom material proper and deriving their nourishment from the organic matter (detritus and bacteria) contained in it). Thus their populations, though probably patchy and scattered, may be expected to be comparatively abundant in individuals. Some catches of porcellanasterids have also yielded a rather large number of individuals (though small in comparison with the number of elasipod holothurians obtained in some deep-sea hauls). Examples are: 32 individuals of *Hyphalaster inermis,* 18 of *Thoracaster cylindratus,* and 86 of *Eremicaster gracilis*. But of course these individuals could have been relatively scattered, since the dredge may have worked over a considerable area.

The three species abundant in individuals, *Hyphalaster inermis, Thoracaster cylindratus,* and *Eremicaster gracilis,* are at the same time (with 32, 20, and 23 finds respectively) some of the most frequently recorded porcellanasterids, and are thus among the dominant abyssal benthic species. The two first-mentioned species are also known to be cosmopolitan. (Incidentally, a world-wide distribution may be expected to apply also to some at least of the abyssal species of porcellanasterids known hitherto from but a single or a few individuals; the species in question being rare and, therefore, more accidentally caught.)

The kind of substratum covering the deep-sea floor (its composition and structure) might be expected to exert some controlling influence on the distribution of the Porcellanasteridae (cf. pp. 207, 212). – Some other marine animals are apparently very sensitive to minute differences in the concentration of various organic and inorganic elements in the bottom substratum as well as in the water (cf. WILSON 1951, URSIN 1960 p. 100). – From the information hitherto available very little can be deduced about this question however.

The Porcellanasteridae are always found on a soft level bottom. In about half of the 110 cases where information is available, the bottom was registered as greyish, greenish, or bluish mud; in about one-third of the cases as ooze (usually globigerina ooze, but in a few cases radiolarian ooze, and in one case diatom ooze), and in one-fifth of the cases as bluish, yellowish, brownish, reddish, greenish, or blackish clay. Finally, in a few cases the bottom was recorded as being of green or black sand. It may be noted, however, that the nature of the bottom recorded may not always have applied to the whole dredged area.

A species such as *Eremicaster gracilis,* in spite of its name a fairly robust form, has been found seven times on a bottom of ooze (globigerina, grey, and diatom ooze), nine times on mud (green, grey, or blue mud), once on clay, and once on sand, – a rather wide range of bottom types. A delicate species such as *Styracaster armatus,* is found exclusively on globigerina ooze (4 finds), whereas the more robust *Styracaster chuni* is recorded exclusively from clay or sandy clay (6 finds, but the kind of bottom was not recorded in two of the cases).

The Porcellanasteridae are mainly known from areas where the deposits are more or less terrigeneous, thus with a fairly high content of organic material. These areas are however, those which have been most extensively dredged, and nothing definite can yet be said about the occurrence of porcellanasterids in other areas. Perhaps the substratum in places may be too soft for these burrowing sea-stars to thrive on, and this in part, could be the explanation for their general absence in the hadal depths.

It should be noted that as early as 1877, WYVILLE THOMSON stated that: "The distribution of life evidently depends in a marked degree either upon the nature of the bottom or upon the conditions which modify the nature of the bottom". To illustrate this he mentioned that "over the vast areas where the calcareous matter of the foraminifera has been removed, and the bottom consists of red or grey clay, animal life is scarce; and is represented chiefly by shell-less orders, such as the Holothurioidea and the Annelids".

A difference in the composition of the bottom faunas in the eastern and mid-Pacific deep-sea on the one hand, and the Atlantic and Indian deep-sea on the other hand, thus (as also touched upon p. 207) may be partly accounted for by the, on the average, somewhat different substrates in these two regions: primarily abyssal red clay in the former region, but calcareous ooze in the latter.

The general impoverishment of the deep-sea bottom fauna with increased distance from land (and from oceanic areas with a high productivity in the photic layer) and also with increased depth, is a phenomenon which was noted early on in the exploration of the deep-sea and has been amply confirmed e.g. by the recent Russian explorations of the Pacific and Indian oceans (cf. FILATOVA 1959 and BELYAEV 1959). However, in the upper abyssal region the Porcellanasteridae apparently gradually replace the bathyal fauna elements extending out there, becoming eventually one of the dominant animals in the lower abyssal zone. Thus the Porcellanasteridae may be fairly uniformly spread over most of the oceanic deep-sea, having their main occurrence at depths of about 4000 m, and disappearing only when the abyssal depths pass into the hadal ones.

10. The possible fluctuations in the abyssal populations

In the deep-sea with its stable ecological conditions and no marked seasonal variations (cf. p. 202), the animal populations probably maintain themselves for very long periods in those areas where they have once become successfully established. As long as a population comprises a sufficient number of individuals it will be almost impossible for a competing form to gain a foothold in the same area. The deep-sea animals allegedly have a considerable longevity and, if this be so, fluctuations in the populations and the composition of the local faunas probably take place only over relatively long periods.

The Porcellanasteridae (especially their young) may be preyed upon by other kinds of sea-stars, crustaceans, or bottom fishes. (In the deepest regions however, they can have only few enemies, if any at all). Further, they may be attacked by parasites, the most damaging being ascothoracid barnacles. Due to these conditions a population of porcellanasterids may be exterminated or the number of individuals so diminished that it becomes possible for a competing form to settle. A population of porcellanasterids may perhaps also simply exhaust the available food-supply and so die off. – Incidentally, extensive areas in the deep-sea may perhaps for long periods be totally or almost barren of life, except for bacteria and protozoa. This assumption seems borne out by the many photographs of the deep-sea floor showing no life nor any trace of life (cf. e.g. LAUGHTON 1959). Desert-like areas in the main Pacific have also been recorded by various deep-sea expeditions (cf. e.g. A. AGASSIZ 1906 p. 9). It may further be noted that the phenomenon of a bottom area "Lying fallow in periods" is also known from the sublittoral zone (cf. THORSON 1957 p. 484).

When a population of porcellanasterids (or other deep-sea forms which feed in a similar way) disappear from a given area, the type of species conquering the vacant space may be completely accidental. The succeeding species will be those, which at the right moment, happen to produce viable progeny. For such reasons, well-defined animal communities comparable to those known from the shallow marginal seas, probably do not exist in the abyssal region. In the Kurile-Kamchatka and Bougainville trenches, over 90 % of the bottom fauna (by weight) consists of the holothurian *Elpidia* *glacialis,* in the Kermadec Trench 70-95 % consists of bivalves, and in the Tonga Trench 50 % consists of amphipods and isopods (BIRSTEIN 1959). It is quite possible that these differences are not a permanent feature. The faunas mentioned may be temporary only and possibly subject to considerable fluctuations over periods of sometimes only a few scores of years. (But of course, the different amount of terrigeneous material and organic material from the upper water layers which settle in the various trenches, will account for some permanent differences in their faunas.)

XV. SUMMARY

The porcellanasterid sea-stars are exclusively deep-sea animals, known only from depths exceeding about 1000 m. Prior to the Galathea Expedition they were recorded from 165-170 dredgings, in a total of 600-650 individuals. Fifteen genera and 57 species were named. The Galathea Expedition brought back 469 specimens obtained in 27 dredgings, and this material formed the main basis for a study and revision (see the preceding paper in this report) which resulted in a division of the group into only 9 genera and less than 25 valid species. One new genus, *Abyssaster,* was erected to embrace some of the species formerly included in *Hyphalaster,* but no new species were found.

In the introduction to the preceding paper a survey on the morphology of the Porcellanasteridae is given, and the characters which may be used taxonomically are discussed. Some notes are also appended on their possible mode of life. Included in the systematic section is, besides the rather detailed description of the Galathea material, references to and discussions of all previously recorded porcellanasterids.

The knowledge gained of the taxonomy and distribution of the Porcellanasteridae has thereafter formed the basis for the present review and discussion on some of the general problems of the abyssal fauna – its geological origin, and especially, the zoogeography of the abyssal region.

The now known distribution of the species of Porcellanasteridae, supports the concept of an essentially cosmopolitan lower abyssal level-bottom-fauna. Six of the 14 species of porcellanasterids known from more than two dredgings, have been found in all three oceans. The greatest difference in the abyssal fauna of porcellanasterids is between the faunas of either side of the American continents (the Atlantic and the East Pacific abyssal faunas respectively). The zoogeographical boundary in the abyssal region, next in importance to that formed by the American continents, is apparently constituted by the ecologically unfavourable mid-Pacific deep-sea, corresponding with the so-called East Pacific Barrier, so important in the zoogeography of the shallow and moderate depths.

The Porcellanasteridae seem to have originated (probably in Late Mesozoic) in the bathyal depths of the Tethys Sea from astropectinid-like ancestors. All three exclusively bathyal genera (two of which may be the most primitive porcellanasterid genera) are confined to the region of the Indian Ocean, which on the whole comprises the greatest number of different forms. Some of the world-ranging species of Porcellanasteridae seem to have a rather confined bathymetrical distribution. The porcellanasterid genera hitherto recorded from the greatest depths are probably the youngest phylogenetically. This and other considerations, support the assumption that in the main the recent abyssal fauna is younger than the bathyal and littoral faunas, and that probably on the whole the ancestors of the oldest types of abyssal animals today, did not invade the abyssal habitat until Early Tertiary.

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HETEROSOMATA (PISCES)

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INTRODUCTION

The Galathea Report only treats animals from depths exceeding 400 m. Therefore, only very few species of the order mostly of littoral occurrence, the Heterosomates, are represented in this paper. The species from the upper layers will be dealt with elsewhere, e.g. all the *Galathea* Heterosomates from 0-400 m of depths taken off West Africa are treated in the Atlantide Report vol. 6 (in press).

All measurements are in accordance with the method described by NORMAN (1934, p. 50).

The present material comprises 45 specimens belonging to 6 species. Two of these, *Chascanopsetta galatheae* and *Azygopus pinnifasciatus flemingi* form a species and a subspecies, respectively, new to science.

The material is in a good condition, preserved in formalin, transferred to alcohol, and is kept in the Zoological Museum, Copenhagen.

Abbreviations used in the systematic part:

Std.l. – Standard length in mm
L.l. – Lateral line
D – Dorsal fin
C – Caudal fin
A – Anal fin
V – Ventral fin
P – Pectoral fin

(In the tables the numbers in the brackets indicate the average value of the character in question.)

Gear:

HOT – Herring otter trawl
SOT – Shrimp otter trawl
ST100 – Sledge trawl, 100 cm broad
ST300 – Sledge trawl, 300 cm broad

For further details see BRUUN (1959).

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BOTHIDAE

BOTHINAE

Bothus pantherinus (Rüppell, 1828)
(Fig. ALCOCK 1890, p. 438)

Psettyllis pellucida Alcock, 1890

Material (1 specimen):
St. 203, (25°36'S, 35°21'E). 1 specimen
Std.l. 38. Depth 660-720 m. Gear: HOT.

Table 1 shows the characters for the type specimen of *Psettyllis pellucida*, the *Galathea* specimen and *Bothus pantherinus* from NORMAN's description (1934, p. 234):

Table 1.

	P. pellucida	*Galathea* specimen	*B. pantherinus* (64 specimens)
Std.l.	38	38	33–210
D	85	91	85–95
A	65	67	67–71
C	17	17	17
V	6	6	6
P	5	9–10	9–11
Head in % of std.l.	21	21	25–30
Depth in % of std.l.	96	90	50–60

There is no doubt that the *Galatheae* specimen and the type of *P. pellucida* are identical. The most diverging character is the number of rays in P, but this may be due to a miscounting made by ALCOCK as the rays are very slightly developed at a std.l. of 38 mm. Moreover, in the literature I have never found a description of a species of the Bothinae with so few P-rays, apart from a few species in which the P are absent.

In the same paper Alcock (1890) described a new species, *Psettyllis ocellata,* which was later found to be synonymous with *Bothus ovalis* (Regan, 1908). These two *Psettyllis*-species can be distinguished from each other among other things by the greater depth of body and the nearly complete lack of pigmentation in *P. pellucida,* characters refound in the *Galathea* specimen.

In his monograph Norman (1934, p. 240) mentioned *P. pellucida* under the treatment of the genus *Bothus,* but it has not been referred to any particular species of *Bothus.* – However, on going through the subfamily Bothinae in the monograph, only very few species show the combination of rays in D, A and P found in the present specimen. When using all the characters from table 1, the only possible species is *Bothus pantherinus.* – Columns 2 and 3 in the Table show a comparison between this species and the *Galathea* specimen. Only the "depth and head in relation to std.l." do not agree, but this may be due to a greater variation during growth in *B. pantherinus.*

Distribution. From East Africa to the Hawaiian Is.

The depth at the station (off Natal) at which the specimen was caught is 660-720 m. The gear used was a herring otter trawl (HOT), and judging from the species of fishes taken together with the present individual, the gear was fishing from the surface to the bottom. It is impossible to tell at what depth this specimen was caught, but it is a surprising catch whether it was taken in the surface layers or at the bottom. If it was caught pelagically, it is one of the few records of a pelagically occurring metamorphosed *Bothus,* and this is in good agreement with the wide distribution of the present species. If the specimen was caught at the bottom, this is the greatest depth hitherto recorded for a species of *Bothus.* According to Alcock (1890), *P. pellucida* was taken at a depth of 15-35 m and after Norman (1934) the deepest record should be 50 m.

Chascanopsetta galatheae n. sp.

(Fig. 1 and plate XIV)

Material (14 specimens):

St. 196, (29°55'S, 31°20'E), 425 m. 1 specimen. Std.l. 240. Bottom: sandy mud with stones. Gear: ST100.

St. 202, (25°20'S, 35°17'E), 575-595 m. 13 specimens. Std.l. 122-285. Bottom: sand. Gear: ST300.

Holotype: P853104 of the Zoological Museum, Copenhagen. Type locality: *Galathea* St. No. 202 (off Natal).

Paratypes: P853091 (St. No. 196) and P853092-P853103 (St. No. 202) all in the Zoological Museum, Copenhagen.

This new species fully agrees with the description of the genus *Chascanopsetta* Alcock, 1894, of which hitherto four species have been described. Two of these, *C. prorigera* Gilbert, 1905 from the Hawaiian Is., and *C. lugubris* Alcock, 1894 (Fig. 2) distributed from Japan westward to the West Indies, are fairly closely related to *C. galatheae.* Still the three species differ from each other in certain respects as shown in Table 2.

In Table 2 the characters of *C. lugubris* originate from examinations of 137 specimens, i.e. 122 from West Africa (Poll (1959) with 115 specimens and Nielsen (1961) with 7 specimens) and 15 specimens from the Indian Ocean (Norman 1934). Of *C. prorigera* only the holotype is known.

Table 2.

	Holotype of *C. galatheae*	*C. lugubris*			*C. prorigera* 1 specimen
		Norman 1934	Nielsen 1961	Poll 1959	
Std.l.	144	–	118–146	–	225
D	126	114–122	115–122	116–121	125
A	89	77–85	81–85	77–84	89
L.l.	181	–	181–195	–	–
Head in % of std.l.	19	19–25	20–22	20–23	24
Depth in % of std.l.	26	25–30	26–33	–	33
Eye in % of head	25	25–27	25–30	26–30	25
Max. in % of head	65	71–77	77–81	67–77	60
Dentary in % of head	82	–	–	–	–

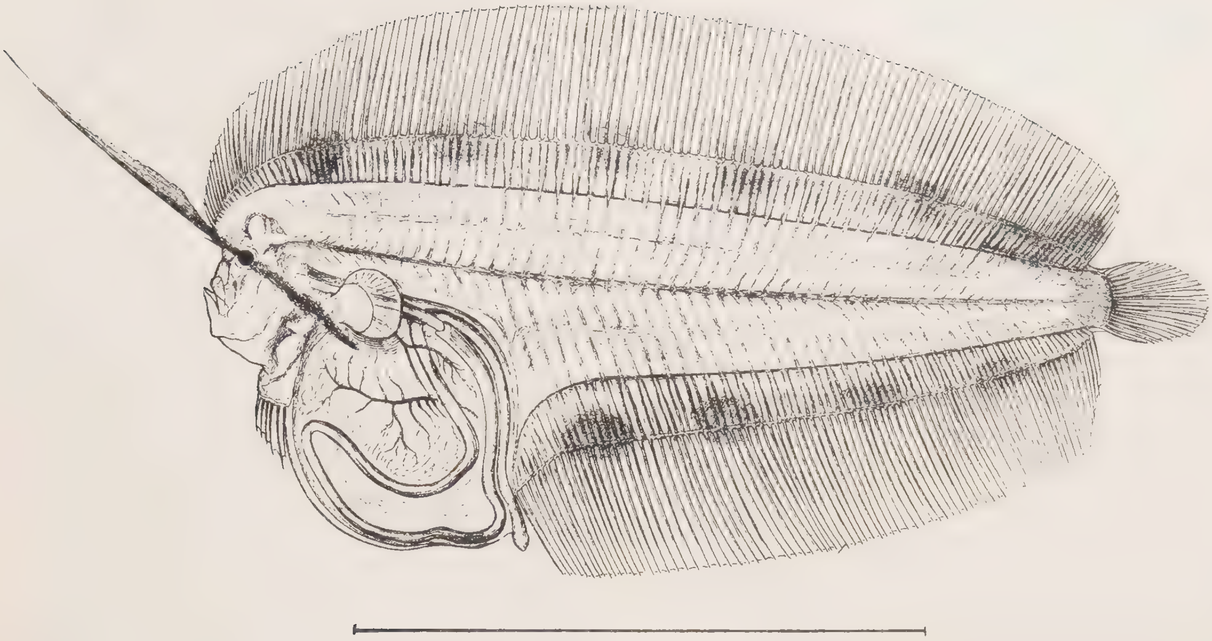

Fig. 1. *Chascanopsetta ?galatheae*, std.l. 78 mm. *Dana* St. No. 3959 III. Caught off South Madagascar. (From BRUUN 1937).

Description:

Holotype. All the meristic and relative characters are shown in Table 2 in comparison with the two species mentioned above.

D commencing just in front of posterior nostril on blind side. The anterior 5-6 rays are a little longer and stouter than the next following. Neither D nor A are coalesced with C. P of blind side only two-thirds of the length of P from the ocular side; both with 14 rays. 17 rays in C. V with 6 rays.

L.l. developed on both sides of body with a low curve over P. The straight part of L.l. about 7 times as long as the curved part. The relation between these two parts of L.l. has been used by NORMAN (1934, p. 250) in separating two species of *Chascanopsetta*. However, this character is so variable that it actually is of no value. For instance NORMAN states that in *C. lugubris* this character is 5 to 5,75 while in *C. prorigera* it is 6; but according to POLL (1959) the character varies from 5,5-6,75 in *C. lugu-*

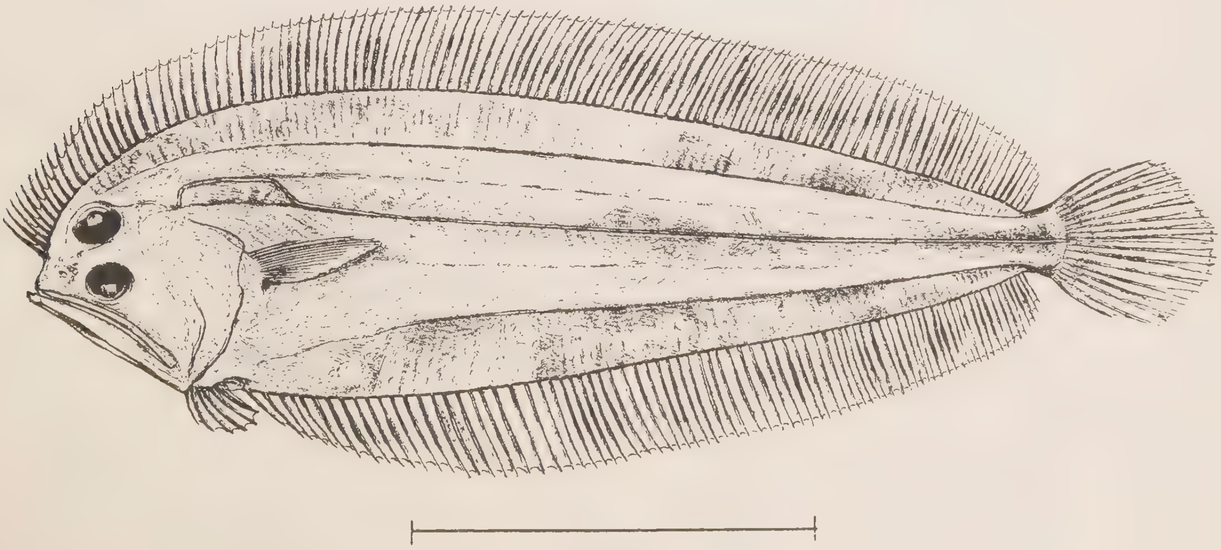

Fig. 2. *Chascanopsetta lugubris*, std.l. 128 mm. *Dana* St. No. 4003. Caught off Sierra Leone. (D 115, A 81). (From BRUUN 1937.)

bris and is thus useless as a character of distinction.

Very small cycloid scales, which cover the greater part of the head too. No scales on the bases of D and A.

Table 2 shows that the proportions of the body of the new species differ much from *C. prorigera.*

The pointed recurvate teeth uniserial in both jaws. Two sizes of teeth placed among each other with relative long interspaces. A large tongue.

No traces of gill rakers on the anterior gill arch.

The colour of the ocular side is light brown and that of the blind side yellowish. The rays of D, C, A and V with black pigment. The peritoneum can be seen through the skin as a dark blue area.

Key to the species of *Chascanopsetta:*

I Length of maxillary never exceeding 80 % of length of head.
  A. Depth of body 40 % of std.l. Number of rays in D 110 . . . *C. megastoma*[1] Kamohara, 1936
  B. Depth of body from 25 %-33 % of std.l. At least 114 rays in D.
    a. Rays in D 114-122. Number of rays in A never more than 85. . . . . *C. lugubris* Alcock, 1894
    b. Rays in D always more than 122 and more than 84 in A.
      1. Head about 25 % of std.l. Depth 33 % of std.l. . . . . *C. prorigera*[1] Gilbert, 1905
      2. Head about 20 % of std.l. Depth in adolescent individuals 25 %-28 % of std.l. . . . . *C. galatheae* n. sp.

II Maxillary and head of the same length . . . . *C. prognathus*[1] Norman, 1939

Variation:

Table 3 shows the variation of the meristic and relative characters of *C. galatheae.* In column A all the 14 specimens are represented, while column B indicates the features of the smallest individual (std.l. 122 mm). Column C and D contain the remaining *Galathea* specimens. Of these all specimens in which the "depth in % of std.l." is larger than 30 are placed in C and the rest in D.

When comparing Table 3 with the figures of *C. lugubris* from Table 2 it appears that the relative characters of the 8 specimens from column D are most in accordance with NORMAN's figures, whereas the individual from B is very different from *C. lugubris* in all characters. Column C holds an intermediate position. In plate XIV an example of each of the three "stages" are figured.

The specimen from B (plate XIV, Fig. a) evidently has a relatively small head, maxillary and eye, a large depth of body and nearly a complete lack of pigmentation. In his monograph NORMAN (1934, p. 33) mentions that typical of young metamorphosed Heterosomates are characters which, apart from the one of the pigmentation, are quite opposite to those found in the present specimen. Still, this specimen could be considered as filling a gap between the unmetamorphosed stage and the fully grown form. This supposition is further supported by the fact that a very large (std.l. 78 mm), still symmetrical larva (Fig. 1) has been reported (BRUUN 1937). It has 126 rays in D and 88 in A, a number which is in accordance with that found in *C. galatheae.* Moreover, the larva was caught off the southwest coast of Madagascar, a position not far from the localities of the present species. This might indicate that the larva belongs to the species *C. galatheae,* and not to *C. lugubris.* – Among the *C. lugu-*

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[1] Only the holotype is known.

Table 3

	Chascanopsetta galatheae			
	A 14 specimens	B 1 specimen	C 5 specimens	D 8 specimens
Std.l.	122–285	122	136–148	143–285
D	122–(125)–127	125	122–123	123–(126)–127
A	84–(87)–89	87	84–(85)–87	86–(88)–89
L.l.	167–(186)–204	179	167–(186)–201	174–(187)–204
Head in % of std.l.	15–(18)–21	15	16–(18)–20	18–(19)-21
Depth in % of std.l.	25–(29)–34	34	30–(31)–32	25–(27)–28
Eye in % of head	17–(24)–28	17	22–(23)–24	24–(26)–28
Max. in % of head	50–(68)–77	50	63–(66)–69	65–(73)–77
Dentary in % of head	67–(85)–93	67	75–(81)–86	85–(90)–93

bris treated in the Atlantide Report (NIELSEN 1961) a specimen is found with a std.l. of 122 mm or exactly of the same length as the individual in column B, Table 3. However, as regards the relative characters, the *Atlantide* specimen agrees best with column D in Table 3, i.e. with the grown up form. To explain this disagreement it may be supposed that the length of the fish is not increasing, but perhaps even decreasing during the metamorphosis of the larva into the adolescent stage, a phenomenon observed within other fish groups. For example when the leptocephalus develops into the elver this involves a reduction of the length.

The remaining 13 specimens are sorted out in the columns C and D in Table 3, showing that the differences are not due to different std.l., even if the three largest specimens (with std.l. from 240-285 mm) all belong to column D. It is rather a question of degree of development. Plate XIV, Figs. b and c show the differences between the two "stages", and it appears that the specimens from column C have many of the characters typical of the individual from column B.

These considerations indicate that the 8 specimens from column D are the only grown up representatives of the species *C. galatheae,* while the rest are adolescent individuals of more or less advanced stages.

Distribution:

This new species has been found at two localities off Natal at depths between 425 and 595 m. If the *Dana* specimen (BRUUN 1937) belongs to this species, also the south end of Madagascar can be included in the area of distribution.

PLEURONECTIDAE

RHOMBOSOLEINAE

Azygopus pinnifasciatus flemingi n. subsp.

(Fig. 3)

Material:

St. 626, (42°10′S, 170°10′E), 610 m. 3 specimens.
Std.l. 86-101. Bottom: glob.ooze. Gear: ST300.

Holotype: P853105 of the Zoological Museum, Copenhagen.

Paratypes: P853106 and P853107 of the Zoological Museum, Copenhagen.

This new subspecies shows all the characters of the genus *Azygopus* Norman, 1926. It is very like the species *Azygopus pinnifasciatus*[1] Norman, 1926, the only described species of this genus. Still, it differs in several characters such as the diameter of the eyes, the number of gill rakers, L.l. scales, etc. (see Table 4), so it seems most correct to describe it as a new subspecies.

Table 4

	A. p. pinnifasciatus	*A. p. flemingi*		
	10 specimens	Holotype P853105	Paratype P853106	Paratype P853107
Std.l.	85–198	94	101	86
L.l.	88–95	110	107	103
Scales between L.l. and highest point of dorsal profile	27–32	36	38	35
D	104–115	103	104	97
A	84–92	86	86	81
P (dextral)	10–11	11	11	12
C	18–19	18	18	18
V (dextral)	10–11	9	9	10
Depth in % of std.l.	39–44	38	41	38
Head in % of std.l.	21–23	24	27	24
Eye in % of std.l.	–	9,6	11	9,2
Eye in % of head	25–30	39	40	40
Max. in % of std.l.	–	5,9	6,5	5,8
Max. in % of head	30–33	25	24	25
Gill rakers	11–12	9	10	9

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[1] By the courtesy of Dr. H. O. FLETCHER, the Australian Museum, it has been possible to make comparisons between one of the paratypes of *A. pinnifasciatus* from the collections of the Australian Museum and the specimens of *A. p. flemingi.*

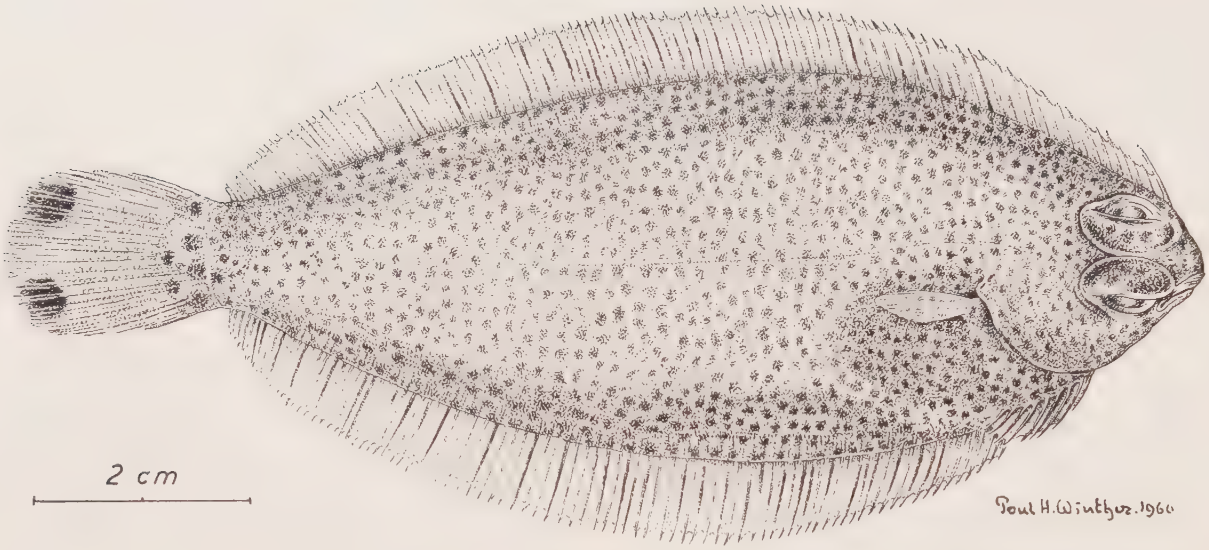

Fig. 3. Holotype of *Azygopus pinnifasciatus flemingi*, std.l. 94 mm. St. No. 626.

Description:

Holotype. All the meristic characters are shown in Table 4 and are compared with *A.p.pinnifasciatus*. In the following description *Azygopus p.pinnifasciatus* is abbreviated to *A.p.pinn.*

D beginning above the posterior nostril of the blind side, the first ray longer than the following, and D with fewer rays than found in *A.p.pinn.* A and D both free of C and both have the basal part covered with scales. Dextral V free of A and situated nearly on the ventral edge, number of rays lower than in *A.p.pinn.* Sinistral V only with 5 rays. P of eyed side about twice as long as P of blind side.

L.l. developed on both sides and forming a slight curve anteriorly. Scales rather small; number of L.l. scales larger than in *A.p.pinn.* More rows of scales between L.l. and highest point of dorsal profile than found in *A.p.pinn.* Head and even eyeballs covered with scales. Ctenoid scales on both sides of body.

Maxillary of eyed side smaller than in *A.p.pinn.*

The small and acute teeth are almost entirely confined to the blind side where they are placed in 3-4 rows.

On the lower part of the anterior gill arch 9 rather short, conical gill rakers are found, 2-3 rakers fewer than in *A.p.pinn.*

Eye diameter much larger than in *A.p.pinn.* The eye balls are quite contiguous. Snout one-third of horizontal eye diameter.

The colour of the eyed side is yellowish with innumerable brownish, irregular spots. The eyeballs are grey-blue, and the posterior part of C has two large, black, circular spots, which can be seen on the blind side, too. Nearly all rays of D and A are brown or have traces of brown colouration. This is also different from *A.p.pinn.* in which the coloured rays of D and A are distributed as 7-8 groups of black rays in each fin. Each group consists of 3-5 rays, and between the groups there are about 10 colourless rays. The blind side is uniformly yellowish in both subspecies.

Variation:

The variation in the meristic characters is shown in Table 4. Furthermore, some small variations in the colouration are found. In one of the paratypes (P853107) the spots on the eyed side are darker and even more densely placed than in the holotype.

Distribution:

This new subspecies has only been found at the type locality in the Tasman Sea off the South Island of New Zealand at a depth of 610 m. The related subspecies *A.p.pinnifasciatus* has been recorded from depths of 200 to 800 m south of Australia. – The localities off New Zealand and South East Australia are separated by the Tasman Sea, a distance of about 2000 km. Most of the distance has depths exceeding 5000 m, so it is a problem how the species *Azygopus pinnifasciatus* has been able to cover this long stretch. One explanation is that unknown sea-mountains in the area have been used as stepping stones. Another explanation may be that the larvae have a long pelagic life, but no larvae of this genus have ever been described. An examination of the vertical distribution of other genera of Heterosomates shows that very few occur at depths lower than 400 m. Furthermore, the larval stage is only known for some of these genera, but in some cases the larvae do have a prolonged pelagic life, e.g. *Poecilopsetta* and *Chascanopsetta* (BRUUN 1937), and some species of *Arnoglossus* and *Symphurus* (KYLE 1913). *Azygopus* may perhaps be another example.

This subspecies was named in honour of Dr. C.A. FLEMING, Wellington, who was a member of the Expedition in the Tasman Sea.

Symphurus ocellatus von Bonde, 1922

(Fig. VON BONDE 1922, pl. I)

Material (14 specimens):

St. 196, (29°55′S, 31°20′E), 430 m. 3 specimens. Std.l. 90-99. Bottom: sandy mud. Gear: ST300.

St. 197, (29°57′S, 31°26′E), 495 m. 1 specimen. Std.l. 100. Gear: SOT.

St. 202, (25°20′S, 35°17′E), 575-595 m. 10 specimens. Std.l. 87-113. Bottom: sand. Gear: ST300.

These 14 specimens all agree – as shown in Table 5 – with the description of *S. ocellatus* (VON BONDE 1922 and SMITH 1953).

Table 5.

	S. ocellatus	*Galathea* specimens
D	95–100	97–(99)–102
A	80–90	84–(87)–89
L.l.	about 85	about 90
Head in % of std.l.	18	18–(19)–20
Depth in % of std.l.	26–30	25–(27)–28

This species is remarkable for the black spot on D and A. The spot covers D from the 80th to the 90th ray and A from 65th to the 75th ray.

Distribution:

S. ocellatus is known to occur off the coast of Natal (about 25°S.lat. – about 33°S.lat.) at depths between 430 m and 640 m, so all the present specimens were taken within the area known.

Symphurus holothuriae Chabanaud, 1948

(Plate XIV, Fig. d)

Material (2 specimens):

St. 423, (10°27′N, 124°18′E), 750 m. 1 specimen. Std.l. 48. Bottom: mud. Gear: ST300.

St. 436, (10°12′N, 124°14′E), 710 m. 1 specimen. Std.l. 45. Bottom: mud. Gear: ST300.

It is with some hesitation that these two specimens are referred to this species. Besides *S. holothuriae* also the description of *S. trifasciatus* (Alcock, 1894) agrees with the present material. Table 6 gives the meristic characters.

This shows that the two species are very much alike. CHABANAUD (1948) states in his description of *S. holothuriae* that this species is closely related to *S. trifasciatus,* but differs in certain respects: The dorsal lobe of the operculum is more developed than the ventral one in *S. holothuriae,* and the ocular side is provided with three broad black cross-bars in *S. trifasciatus*. The latter difference is perhaps due to the fact that the specimen upon which CHABANAUD described the new species was caught in 1882. The long time of preservation (56 years) may have bleached the cross-bars originally present. It may be that even a shorter stay in formalin and alcohol is sufficient to delete the cross-bars. The *Galathea* specimens have been kept in formalin for about 10 years and one of the specimens has some very diffuse colour marks on the eyed-side (see Plate XIV), which possibly can be interpreted as faded bars.

CHABANAUD also states as a reason for consider-

Table 6

	S. holothuriae	*Galathea* specimens	*S. trifasciatus*
D	84	86–88	85–91
A	70	74–76	71–78
L.l.	about 80	about 80	80–82
Head in % of std.l.	24	27–28	about 25
Depth in % of std.l.	26	27–28	about 25
Eye in % of head	12	11–12	–
Snout in % of head	25	23–25	–

ing the specimen forming a new species that the type locality of *S. holothuriae* northwest of Australia is very far from that of *S. trifasciatus* in the Gulf of Bengal. However, the seas between have large areas with depths less than 500 m. Thus it should be very easy for a species, under these conditions, to spread over this long distance. Several species within the Cynoglossidae are distributed over even larger areas.

These considerations indicate that *S. holothuriae* is probably a synonym for *S. trifasciatus*, but until more and especially fresh material of *S. holothuriae* has been procured, nothing definite can be stated.

Distribution:

The only hitherto known specimen, the holotype, was taken on the Holothurian Bank northwest of Australia, and the two *Galathea* specimens originate from the Philippines off Cebu.

Cynoglossus (Trulla) zanzibarensis Norman, 1939
(Fig. Norman 1939, p. 105)

Material (11 specimens):

St. 196, (29°55′S, 31°20′E), 430 m. 1 specimen. Std.l. 148. Bottom: sandy mud. Gear: ST300.

St. 197, (29°57′S, 31°26′E), 595 m. 10 specimens. Std.l. 118-173. Gear: SOT.

These specimens do not agree with any of the Heterosomates from South Africa mentioned by Smith (1953), but as shown in Table 7 they are identical with the more northerly species, *Cynoglossus zanzibarensis*. Furthermore, the following characters agree with the description of *C. zanzibarensis:* The ocular side with a single tubular nostril in front of the lower eye (typical of the subgenus *Trulla* Kaup, 1858). Three L.l. on the ocular side and none or one very indistinct L.l. on the blind side.

Table 7

	C. zanzibarensis 6 specimens	*Galathea* specimens 11 specimens
D	116–122	120–(122)–124
A	94–100	98–(99)–103
Scales in middle L.l.	about 75	80–85
Number of L.l.	3 + 0	3 + 0
Scales between middle and upper L.l.	13–14	12–(13)–14
Head in % of std.l.	21–22	20–21
Depth in % of std.l.	25–26	22–(23)–24
Eye in % of head	13–14	11–(12)–15
Snout in % of head	about 30	29–(30)–35

The difference in the number of scales in the middle L.l. may be due to the difficulty in making an exact counting since none of the specimens had all the scales preserved.

Distribution:

Earlier only known from two localities in the Zanzibar area, at depths of 183-293 m. This new record, nearly 3000 km south of the type locality, can easily be explained by the currents off East Africa. When the South Equatorial Current reaches the African continent, part of it turns southward and continues along the coast to the Cape Province as the warm Agulhas Current.

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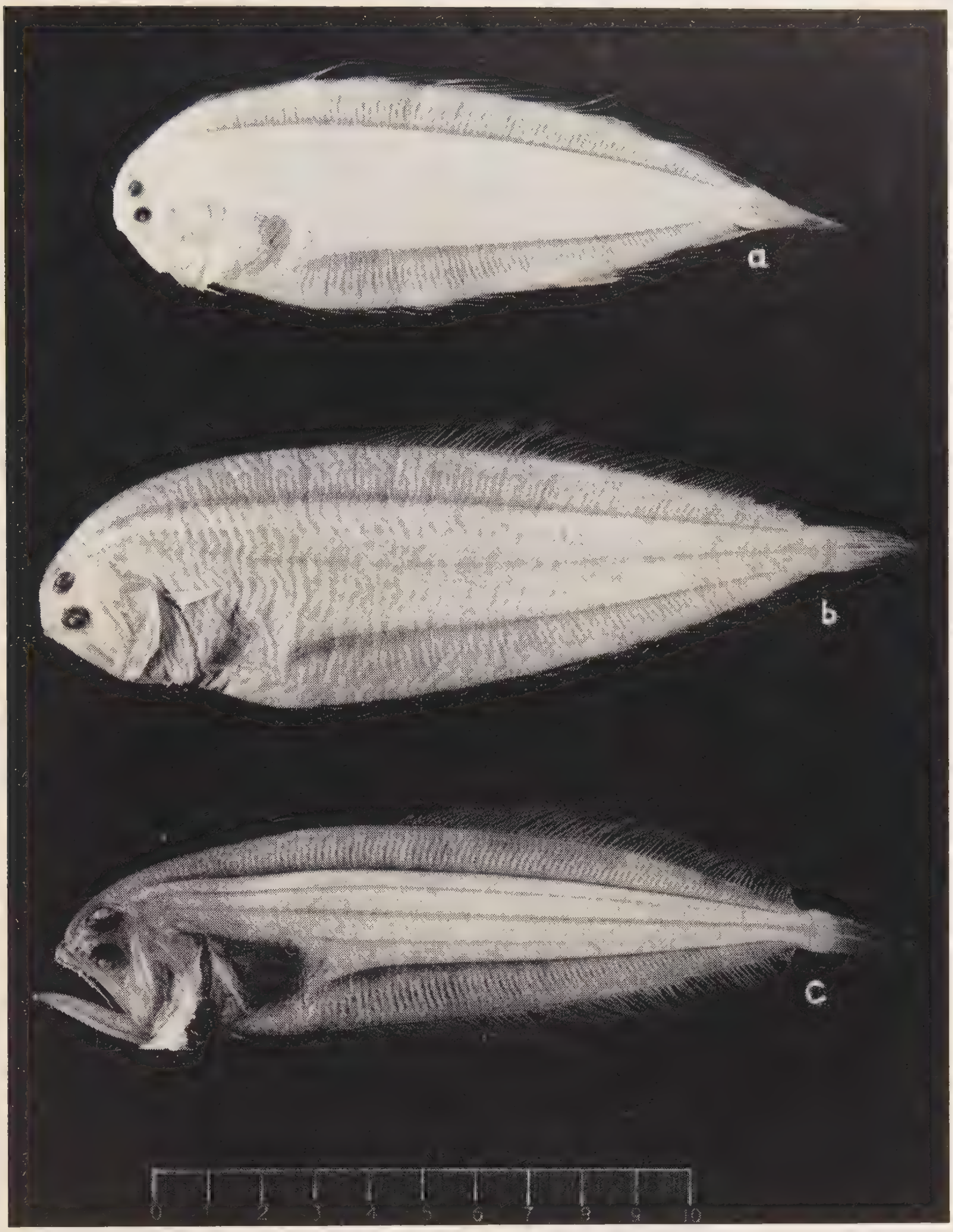

Fig. a. Paratype of *Chascanopsetta galatheae*, std.l. 122 mm. St. No. 202. (An example of column B, Table 3).
Fig. b. Paratype of *Chascanopsetta galatheae*, std.l. 148 mm. St. No. 202. (An example of column C, Table 3).
Fig. c. Holotype of *Chascanopsetta galatheae*, std.l. 144 mm. St. No. 202. (An example of column D, Table 3).

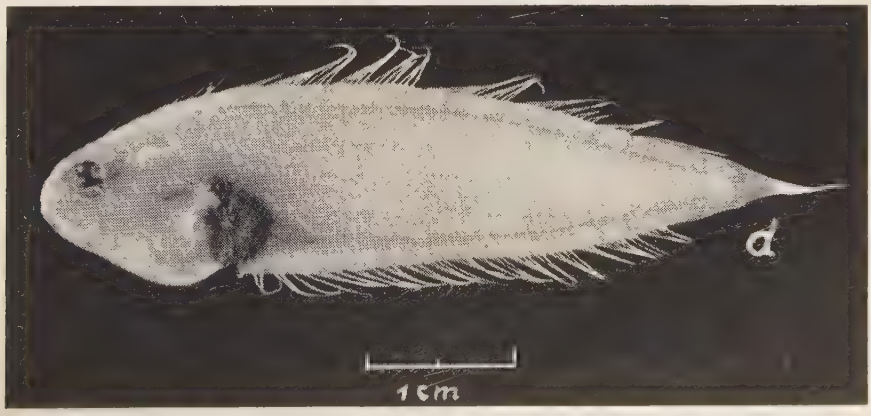

Fig. d. *Symphurus holothuriae*, std.l. 45 mm. St. No. 436.

LIST OF PAPERS RESULTING IN WHOLE OR IN PART FROM

THE GALATHEA DEEP-SEA EXPEDITION ROUND THE WORLD 1950-52

(Supplementary to the list given in the Introduction to vol. 1, 1959, pp. 18-19).

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